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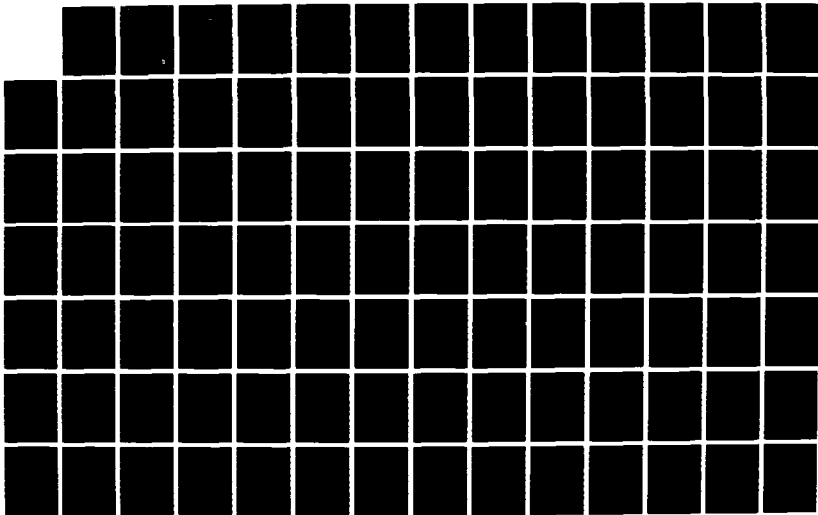
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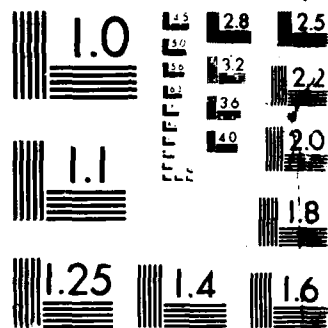
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FINAL REPORT

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The effect of acid deposition on potentially sensitive soil-plant systems at
Vandenberg AFB, California.

Submitted by:

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(619-265-6328)

30 April 1988

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Introduction

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We thank the many persons at Vandenberg AFB who facilitated our work there. The Environmental Task Force deserve special thanks, particularly Jim Johnston, Chuck Pergler, Mike McElligott, and Rich Nichols. We were assisted at various stages by civilian and military Air Force Personnel from other installations. Lt. Col. Russ Rudolf deserves special notice for help at a critical stage of the work.

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PART 1

FIELD SURVEY OF SOIL PROPERTIES AND VEGETATION COMPOSITION ON
FOUR SOIL TYPES AT VANDENBERG AIR FORCE BASE

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SITE SELECTION

A topographic transect running from stabilized dunes through a chronosequence of progressively older sandstone terraces, and ending in a shale-derived soil, was established on South Vandenberg Air Force Base near Cable Road between SLC-4 and the Scout Launch Complex near Avery Road (Fig. 1). The Santa Lucia (shale-derived), Tangair, Baywood and Dune soils occur, respectively, from the highest to the lowest topographic position. The transect is located about 3km from the space shuttle launch site (SLC-6). Possible transect locations closer to the launch site were investigated but rejected because one or more soil types were missing or poorly represented, the vegetation was badly disturbed on one or more soil types, or both. Sampling at this distance from the launch facilities in no way affects the goals of the project, which emphasize an experimental evaluation of sensitivity of these soils and their associated vegetation to pulses of highly acidified water.

SOIL STUDIES

METHODS

The 4 soil types along the chronosequence were described and samples collected from 5 soil pits on each soil type. The pits, approximately 1m x 2m were dug to a depth sufficient to reach the C horizon or the underlying bedrock. The soil pits were located immediately adjacent to the vegetation transects. Soil depth, color, structure and other morphological features were recorded in the field. Samples, replicated a least twice, were collected from each horizon. These were analyzed for the physical and chemical properties at the University of Alaska Soils Laboratory and at The Biology Department, San Diego State University.

RESULTS

Detailed results are presented in Part 4 of this report. However, the results confirm the progression in soil development from the youngest to the oldest terrace in the sand-derived soils. As expected, the B horizon is absent in the recently stabilized dunes, present but poorly developed in the Baywood soil, and well developed in the Tangair. With increasing silt plus clay content increases in iron concretions form, approaching a hardpan in the most extreme examples of the Tangair.

The Santa Lucia soil is formed in the diatomaceous shale bedrock, in contrast to the other three sand-derived soils. Like the sand soils, the Santa Lucia is acidic, but it differs in nearly every other characteristic. Of special significance is the higher organic matter content and the much greater cation exchange capacity. Both these differences would tend to increase the buffering capacity of the Santa Lucia relative to the sand soils. The substantially finer texture of the Santa Lucia soil, with some horizons have more than 30% clay, is one of the main reasons for the higher exchange capacity. By increasing water holding capacity, the finer texture would also tend to restrict the effects of acid additions to the upper soil layers.

VEGETATION COMPOSITION

METHODS

Vegetation transects were established in January 1985 and sampled in June 1985. The arrangement of the transects along the topographic sequence is shown in Figure 1. The original plan was to sample 200m of line transect on each soil type, but because of variability in the vegetation on Santa Lucia and Tangair soils, an additional 200m was added.

Along each transect the crown cover of each species was measured to the nearest centimeter. Overlap was considered, so the total crown cover can sum to greater than the length of the transect. Living and dead canopy was recorded. A crown intercept was considered living if there were live leaves or branches present, even if there were also dead branches within the same intercept. Canopy was classified as dead when there were only non-living branches present. Live canopy therefore includes a variable proportion of dead branches. The height of the canopy was recorded every 2m and the species of greatest height noted. From these data total crown cover for each species, the relative frequency of each species as the top layer of the canopy and the total amount of area not covered by shrub canopies was estimated.

RESULTS

The area of the topographic transect, except perhaps for most parts of the Dune site, was burned in 1977. The data therefore reflects the vegetation at an early stage of recovery after fire. These data are summarized in Table 1.

The Dune site was characterized by a mosaic of depressions and ridges which have distinctive vegetation assemblages. The ridges have a sparse cover of mat-forming perennial herbs, succulents (e.g. Dudleya spp.) and sub-shrubs (e.g. Lotus scoparius). The depressions have a more or less dense cover of mostly drought deciduous shrubs (Artemesia californica, Lupinus chamissonis) and some evergreen species (Haplopappus ericoides). Overall cover was sparse with about 50% cover of live crowns at the time of the sample. The vegetation on the Baywood Soil was a well developed coastal sage scrub dominated by the drought-deciduous Artemesia californica and the evergreen but relatively soft leaved Haplopappus ericoides. Some sub-shrubs (Lotus scoparius) and herbs (Scrophularia atrata) were also

abundant. A substantial proportion of the crown cover was dead shrubs. This mortality cannot be considered simply thinning, since the live plus dead cover was substantially greater than the live cover alone. It appears that the vegetation is declining from a peak of abundance and density, perhaps stimulated by higher fertility after the 1977 fire.

The Tangair Soil was divided into two sample sites. The lower site was more typical of coastal sage-scrub vegetation, and was dominated by Baccharis pilularis, Lotus scoparius, and Rubus ursinus. Artemesia californica and Salvia mellifera were also conspicuous. In the upper portion of the site, these sub-shrubs were largely replaced by more longer lived species typical of hard chaparral vegetation, such as Ceanothus thrysiflorus, Ceanothus impressus and Rhamnus californica. Salvia mellifera continued to be important on these upper slopes as well.

The Santa Lucia Soil was divided into 2 sample sites. The east site was dominated by a sage-scrub vegetation in which large patches of senescent Lupinus arborea were conspicuous. Chaparral elements (Adenostoma fasciculatum, Ceanothus ramulosus, Arctostaphylos pechoensis) were also present and dominated an adjacent area, suggesting that the area sampled may have been disturbed in the past. The west site had many of the same species, but a much denser cover of herbs. Areas without shrub cover were mostly covered with a dense turf of mixed herbs and annual and perennial grasses. The shrub canopy was multi-layered and complex. The uppermost layer was dominated by Salvia mellifera, Artemesia californica and Baccharis pilularis. Beneath this drought-deciduous layer was a sub-canopy of Rubus ursinus, Rhamnus californica and other low growing species.

The leaf phenology of the shrub species growing at Vandenberg may be an important variable affecting degree of damage resulting from direct depositional

effects, as well as the acidity of fallout reaching the surface of the soil. Deposition events that occur when the deciduous species are fully developed are likely to have a very different effect than deposition that occurs when these species are mostly leafless. Presumably deposition would also be more harmful to species when they are in the early stages of active growth after the first fall rains and in the periods of most favorable moisture and temperature later in the winter. For similar reasons the vegetation may be particularly susceptible in the early post-fire recovery period.

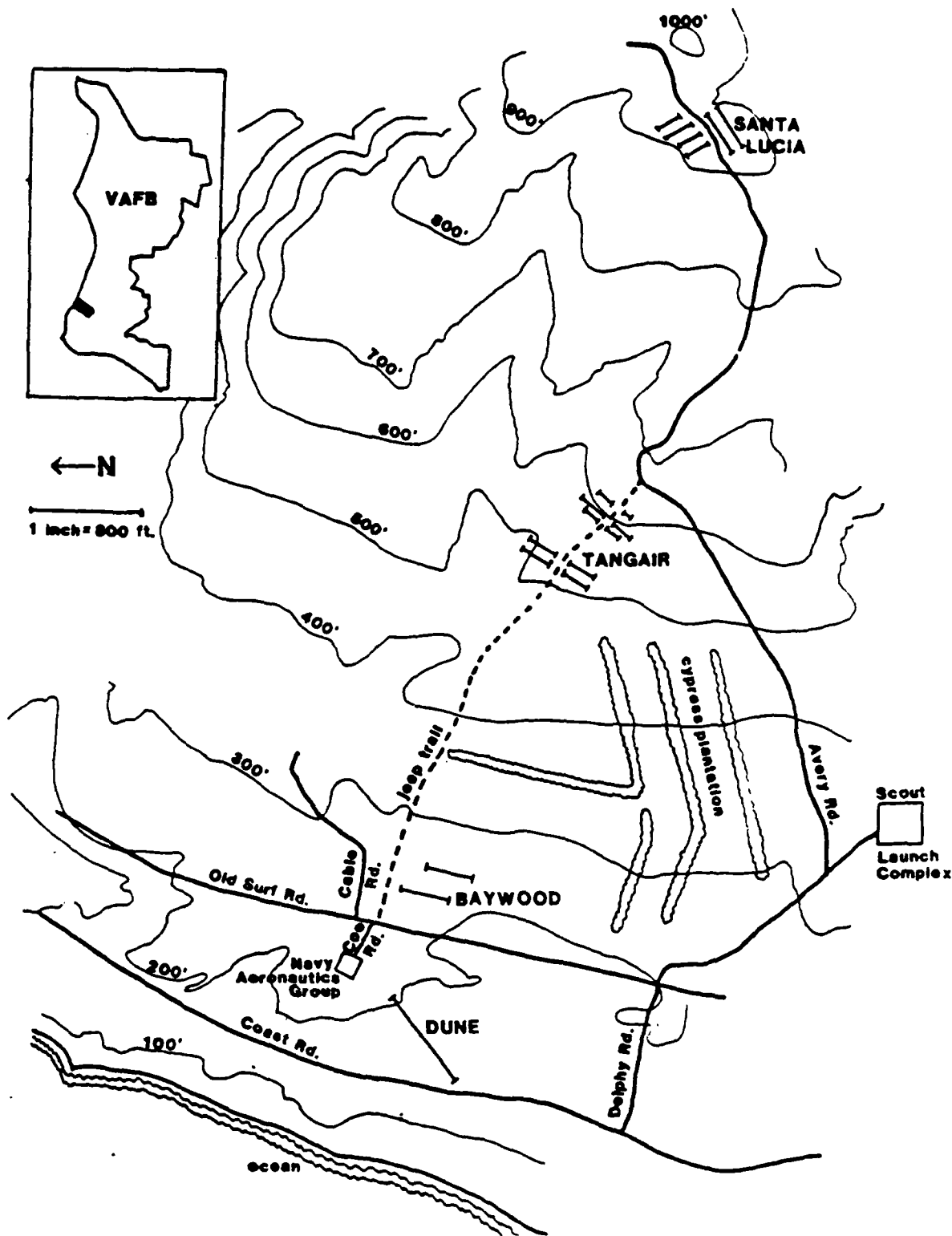


Fig. 1. Map of the study area on Vandenberg Air Force Base, showing the location and elevation of the vegetation transects on the four soil types.

SPECIES	DUNE		BAYWOOD		TANGAIR				SANTA LUCIA			
					UPPER		LOWER		EAST		WEST	
	L	D	L	D	L	D	L	D	L	D	L	D
Adenostoma fasciculatum					1.15	0.0			.06	0.0		
Arctostaphylos pechoensis					3.74	0.0			0.18	0.0		
A. rudis					1.92	0.0						
Artemisia californica	4.06	1.55	10.52	7.3	5.05	0.0	10.97	0.88	25.28	0.25	4.17	0.0
Baccharis pilularis			1.89	0.1	3.9	0.0	20.66	4.21	20.63	0.0	23.07	0.0
Carpobrotus edulis	21.38	3.95	7.69	0.1	6.32	0.0	6.1	0.0				
Ceanothus impressus					18.44	0.57			0.73	0.0		
C. thrysiflorus					38.29	0.13	0.6	0.0				
C. ramulosus					2.37	0.0			0.68	0.0		
Coreopsis gigantea	2.38	0.0										
Cupressus macrocarpa							6.11	0.0				
Dudleya sp.	0.62	0.0					0.08	0.0				
Elymus condensatus												
Eriogonum parvifolium	2.85	1.12					0.78	0.0	0.22	0.09	5.66	0.0
Eriophyllum staechadifolium							0.13	0.0	10.36	0.47	3.26	0.05
Haplopappus ericoides	7.44	3.35	15.62	3.6	0.26	0.0	0.13	0.0	0.26	0.0	0.17	0.22
Helianthemum scoparium					2.55	0.11	8.91	1.09				
Herrea elongata			0.18	0.0	4.14	0.0			0.11	0.0		
Lotus scoparius	2.96	5.31	2.11	0.94			14.91	5.12	2.03	1.05	6.42	0.19
Lupinus arboreus	5.42	8.02							3.09	11.37		
Lupinus albilfrons			0.43	1.79								
Mimosa sp.	0.0	0.43										
Mimulus sp					0.98	0.01	3.09	0.0	1.91	0.0	12.73	0.0
Pteridium aquilinum					0.75	0.22			0.64	0.0	4.19	0.0
Rhamnus californica					20.34	0.04	1.8	0.0	0.05	0.0	25.23	0.54
Rubus ursinus					0.43	0.0	19.41	0.39	1.38	0.0	10.71	0.0
Salvia mellifera					29.25	0.02	12.77	0.0	27.26	0.25	12.23	0.0
S. spathacea			7.94	3.22					0.23	0.0	0.62	0.0
Scrophularia californica												
Senecio blochmaniae	1.21	0.0			1.16	0.0					1.14	0.0
Toxicodendron diversiloba												
Vaccinium ovatum												
Herbaceous	0.78	0.4	9.55	0.0	0.2	0.0	4.44	0.0	14.6	0.0	26.94	0.28
Total cover%	49.1	23.77	75.93	5.9	90.09	0.56	86.37	6.45	85.86	5.74	98.38	0.57

PART 2

GERMINATION RESPONSE TO EXTREME ACIDITY: IMPACT OF SIMULATED
ACID DEPOSITION FROM A SINGLE SHUTTLE LAUNCH

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Abstract--Shuttle launches deposit highly acidified (pH 0.5 - pH 2.0) water vapor into neighboring natural vegetation. A series of experiments which determine the impact of a single simulated acid deposition (SAD) on native species from four soil types found at Vandenberg Air Force Base, California are reported here. Seedling survival and yield, seed germination and seedling emergence from each soil type were investigated. A single, extreme SAD (pH 0.5 and 1.0) prevented seedling establishment in all three species tested, while SAD of pH 2.5 reduced survival and yield. The germination responses of seven species was significantly reduced by a single SAD of pH 1.0, however, the magnitude of this reduction varied widely between species and also within a species on different soils. The moisture status of seeds also influenced germination response, but there was no consistent pattern. In addition, there was a slight germination enhancement in some species after a single exposure to SAD of pH 2.0. The number of seedlings that emerged from field collected soil was not significantly influenced by a single SAD under greenhouse conditions. These results suggest that germination, survival and yield in most species may be reduced after each shuttle launch, if other conditions for seedling establishment are suitable. However, species-specific levels of seed dormancy, temperature and soil moisture conditions and the frequency of launches will also influence seedling establishment.

INTRODUCTION

Each space shuttle launch deposits about 60 tons of hydrogen chloride gas and about 87 tons of aluminum oxide particles into the surrounding environment, carried in water vaporized during the launch^(11,21). The acid deposition from such a cloud of water vapor is different from other forms of acid rain in several ways. First, the acidification is primarily due to hydrochloric acid, although other compounds

are also present⁽¹²⁾. Second, the pH of the vapor is around pH 0.5 in the vicinity of the launch site, and is usually diluted rapidly with distance, although long-distance effects have been recorded^(12, 22). Third, acid depositions are episodic over time; they occur only as often as launches occur.

The long-term stability of vegetation exposed to such extreme acidification may be influenced by the resilience of the soil seed bank. Seed banks represent the genetic persistence of lineages over time and extreme acidification may influence the survivorship of particular seed taxa and so have the potential for altering floristic composition through local extinctions. The rate of floristic change will most likely be driven by species-specific responses to acidification and their interaction with soil conditions, the frequency of launches and climatic conditions before and immediately after launches. The vegetation of semi-arid regions may also be more susceptible to pulses of acidity. The coastal grasslands and shrublands around the launch site at Vandenberg AFB are subject to prolonged seasonal drought and periodic fires. Annual species of grasses and herbs are prominent parts of the vegetation. After fire, many of the shrub species regenerate largely from dormant seed. There is the possibility that launches at or shortly before suitable times for germination, especially after fire, may cause significant mortality among seed regenerating populations. This in turn could cause major shifts in species composition, and in the worst case, a significant loss of plant cover.

Three experiments conducted under controlled conditions are reported here. The first compared seedling survivorship and the yield of survivors after a single simulated acid deposition (SAD) in three native species. The second determined the germination response of an additional seven native species to a single SAD on the soil type which supported each in our study area. Species found on several soils

were exposed to SAD on each. The third determined the impact of a single SAD on the number of seedlings that emerged from field-collected soils.

METHODS

Study area and species selection.

Vandenberg Air Force Base, on the central California coast about 240 km north of Los Angeles, is the proposed site for military shuttle launches. The vegetation within the base is made up of a mixture of dune, coastal sage, chaparral, grassland and tree communities⁽³⁾. Rainfall is confined to winter months but coastal fog represents an additional source of moisture. Our study sites were in the southern area of the base, about 8 km north of the proposed shuttle launch facilities. Survey areas were selected in each of four distinct soil types: Dune, Baywood, Tangair and Santa Lucia soil series⁽²⁾. These soils differ significantly in most of their physical and chemical properties⁽²⁴⁾. However, the Dune, Baywood and Tangair soils are all dune-derived sands differing in age and therefore profile development. Santa Lucia is a clay loam derived from shale and includes a large proportion of shale fragments. Mean soil pH for the four soils are; Dune $4.79 \pm .39$, Baywood $5.93 \pm .38$, Tangair $5.75 \pm .36$ and Santa Lucia $4.99 \pm .43$ ⁽²⁴⁾. At least one representative species from each soil type and a common species found on several soils were selected for study⁽²⁴⁾. Distributions and descriptions of the selected species are presented in Table 1.

Experiment 1: The impact of SAD on seedling survival and pot yield.

This experiment, conducted in an unheated greenhouse, was laid out as a randomized block design with two treatment factors, soil type (Dune, Baywood, Tangair and Santa Lucia) and SAD level (pH of 0.5, 1.0, 2.5 and 5.6). All SAD treatments were prepared from 1.0 N hydrochloric acid by appropriate dilutions with deionized water. Pots were the experimental unit and there were four 8.0 cm free-draining pots per treatment throughout. Each pot was filled with 160 g of the appropriate, air-dried soil and 50 seeds were lightly pressed into the soil surface. Separate experiments were conducted on seeds from three species, Mimulus aurantiacus, Artemisia californica, Baccharis pilularis, all of which were common in our field sites. For each experiment 60 ml of the appropriate pH solution was added to each pot. Controls received deionized water (pH 5.6). This volume of water brought all soils to field capacity. Thereafter each pot was regularly watered with deionized water. The number of seedlings that were alive after 30 days was determined. The above ground biomass from each pot was harvested, dried at 80°C and weighed to provide a measure of yield per pot. Transformed ($\log(x+1)$) results for each species were analyzed by two-way ANOVA. Soil pH was measured after all seedlings were harvested.

Experiment 2: Impact of SAD on seed germination.

Bulked seed samples were either collected from the field sites or were obtained from a commercial seed supplier (S & S Seeds, Carpinteria, California). The commercial seeds were collected from native populations. Preliminary trials were done to determine the conditions that maximized germination. Most species germinated best at 15°C, although some did equally well at 20°C. Lotus scoparius, a

hardseeded species, had higher germination after seeds were exposed to heat (120°C/5 min). Seeds of this species were heat-treated before exposure to SAD.

The SAD experiment, repeated for seven species, was also laid out as a randomized block design with two factors: SAD level (pH of 1.0, 2.0 and 5.6) and seed moisture condition (air-dry or imbibing water). The volume of acidified water applied to each experimental unit was based on an estimate of deposition after shuttle launches at the John F. Kennedy Space Center, Florida (0.144 ml of pH 1.0 HCl/cm²). This estimate represents about 50g Cl⁻¹/m², and corresponds to chloride deposition about 200 m from the launch facilities. We chose this level of acidification for use in our experiments because it approximated the mid-range of chloride deposition at Kennedy Space Center (maximum was 100 g/m²)⁽²²⁾. Experiments on each species were conducted on the appropriate soil, collected from the field sites. All soils were sieved (3 mm) and autoclaved (125°C/60 min) to kill whatever seeds the soil contained. The experimental unit was a free-draining flat (20 x 10 x 5 cm) containing 500 g of the processed soil and 25 seeds laid on the soil surface. These flats were placed in two trays (75 x 75 cm), 12 to a tray, for a total of 24 flats for each species. One tray of 12 flats was allocated to a wet treatment, the other tray to a dry treatment. For the dry treatment, the dry soil surface of each flat was misted with 20 ml of acidified, deionized water. Three SAD levels (pH 1.0, 2.0 and 5.6) were each replicated four times. In this treatment seeds on the soil surface would have low moisture content at the time of exposure to SAD. Immediately after applying this treatment 4 l of deionized water were added to the tray to bring soil in each flat to field capacity. For the wet treatment the soil in each flat was first misted with 20 ml of deionized water to initiate imbibition, and 20 ml of the appropriate SAD was applied 24 hr later. This treatment represented moist field conditions, seeds would have imbibed water before acidification. Experimental flats were never watered from above. Deionized

water (4 l) was added to each tray as required. Soils remained at field capacity throughout the experiment. Most species showed a preference for germination at 15°C, so all experiments were conducted in a 15°C growth chamber.

The number of germinated seeds were scored and removed every day. When no further germinations occurred for 4-5 consecutive days all remaining seeds were removed and tested for viability using 0.05% tetrazolium chloride, which distinguished dormant from dead seeds among the ungerminated fraction⁽¹⁵⁾. However, some of the very small seeded species (e.g., *Artemisia californica*) were impossible to find in the wet soil matrix and were not tested for viability. Percentage germination for each species was analyzed by two-way ANOVA after arc-sine transformation.

Experiment 3: Impact of SAD on the number of seedlings recruited from soil.

Two soil samples were collected at 1 m intervals along 30 m transects placed into vegetation on each of the four soils in the study area. Metal soil canisters were used for sampling (7 cm diameter x 4.7 cm deep) and sample-pairs from each 1 m interval were pooled. Soils were air-dried and sieved (3 mm). The design of this experiment was identical to that of the germination experiment outlined above. Each flat was filled with 700 g of washed river sand and 100 g of sieved sample soil was spread evenly over the sand to a depth of about 0.5 cm. Soil samples used for this experiment were drawn randomly from the sample of 30 from each transect. Sets of 12 flats were placed in trays as before. Eight trays, two for each soil type, contained 12 flats each. One tray from each soil type was designated a moist treatment and the other a dry treatment. For the dry seed treatment 20 ml of acidified, deionized water was sprayed over the soil surface (pH 1.0, 2.0 and 5.6). For

the moist seed treatment each tray was filled with 4 l of deionized water and the soils in flats allowed to take up water over several days. Acid treatments were then applied. The number of emergent seedlings was recorded from each flat each week at which time all flats were randomly repositioned. This experiment was conducted under greenhouse conditions from 17 March to 28 April 1987. No further germinations were recorded after 21 April 1987.

RESULTS

Experiment 1: The effect of SAD on seedling survival and pot yield.

No seedlings of any of the species investigated here survived 30 days after a single SAD of pH 0.5 and pH 1.0. Soil pH values for all SAD treatment levels are given in Table 2. The influence of SAD and soil type on seedling survival and pot yield was determined for the pH 2.5 and control treatment (pH 5.6) for each species in turn.

(a) Seedling survivorship

More M. aurantiacus than B. pilularis and A. californica seedlings survived for 30 days on all soils after a single SAD of pH 2.5 (Fig. 1a). For M. aurantiacus, soil and SAD independently influenced the number of seedlings that survived (Table 3a). The number of B. pilularis seedlings that survived was only influenced by soil, while in A. californica the interaction between soil type and SAD significantly influenced seedling survival (Table 3a, Fig. 1a).

(b) Pot yield

Yield (biomass per pot) was significantly influenced by soil in all three species, but a single SAD of pH 2.5 significantly reduced the pot yield in A. californica only (Table 3b). In general, yield was greatest on the Santa Lucia soil and lowest on the Dune soil (Fig. 1b). The yield of A. californica was greater than that of the other two species on all soils except the Dune type, where M. aurantiacus was more productive (Fig. 1b).

Experiment 2: Impact of SAD on seed germination.

Germination was significantly reduced after a single SAD of pH 1.0 in all species except Scrophularia californica (Tables 4, 5). However, the magnitude of the response varied markedly between species, SAD level and seed moisture condition (Table 5). There was no consistent germination response to the pH 2.0 treatment. Neither was there a strong tendency for acidification to increase germination in any of the species tested here, although some evidence exists. For example dry A. californica seeds on Baywood soil exposed to pH 2.0 produced significantly higher germination than did the control (Table 5: unplanned comparison $F_{5,18} = 46.90$, $P < .001$). In general, lower germination in the extreme SAD treatment was the result of a higher proportion of dead seeds, as determined by tetrazolium test, rather than changes to the ratio of germinable and dormant fractions.

In only four cases was there a significant interaction between the moisture status of seeds and SAD (Table 4). Three were found in A. californica; on Dune, Baywood and Tangair soils respectively (Table 4). It is clear that the germination response of A. californica was influenced by soil type at all SAD levels, but seed moisture status was only significant at pH 2.0 (Table 6).

There was no change in germination rate after SAD in all species except Bromus diandrus, where SAD of pH 1.0 spread germination over four times the time taken by controls (16 days vs. 4 days).

Experiment 3: Impact of SAD on the number of seedlings recruited from soil seed banks.

Seedling density was significantly influenced by soil type ($F_{3,72} = 180.8$, $P < .001$): the Baywood soil supported 26.4 ± 6.7 seedlings, Tangair 13.3 ± 14.5 seedlings, Santa Lucia 9.8 ± 3.7 seedlings and Dune 1.5 ± 1.4 seedlings per 100 g of soil. However, there was no significant change in the number of emergent seedlings after a single SAD ($F_{2,72} = 2.12$, NS), and the effect of SAD on seedling emergence did not interact significantly with soil type ($F_{6,72} = 0.41$, NS). In this experiment we did not attempt to identify the seedlings.

DISCUSSION

Our objective in this study has been to determine the impact of a single SAD on the seed reserve of vegetation in the vicinity of the shuttle launch facility at Vandenberg Air Force Base. Overall, our results indicate that under favorable conditions for seedling recruitment, the proportion of germinating seeds will be reduced by a single exposure to pH 1.0, and that survivorship among these will be negligible. Exposure to pH 2.0 will not significantly reduce the germinable fraction, but may stimulate germination in some species. However, exposure to a single SAD of pH 2.0 is likely to reduce seedling survivorship and yield. Soil type and seed moisture condition will also influence the impact of a single SAD on germination.

Many of the species investigated in our study produce a mixture of dormant and germinable seeds, but the impact of acidification on the dormant fraction is not known. It is likely that the general response of this fraction will be an acceleration in the rate at which seeds become germinable. Exposure to acid is a well accepted technique for breaking seed dormancy in the laboratory^(14,23).

Other workers, investigating the effects of acid rain, have demonstrated some reduction in germination after continual exposure to pH 2.0-3.0, and significant interspecific variation in the degree of response among coexisting species^(9,13,17,20). Our results illustrate that a single exposure to more extreme acid conditions reduces the apparent tolerance of seeds, but interspecific variation is still present. In addition, germination rate under controlled conditions is not generally influenced by a single SAD. A similar result had been reported for tree seeds exposed to continual acidification⁽²⁰⁾. Numerous authors have demonstrated that germination response is less sensitive than is subsequent seedling growth to acidification^(10,13,17,18,19). Although it is common for continual acidification, under controlled conditions, to stunt seedling size and induce morphological changes to leaf structure^(1,4,6,9,13,18), it is not clear what the consequences of these changes are for seed production and therefore the persistence of lineages. It may be that, over time, seedlings exposed to acidified precipitation will develop into seed-producing plants, albeit more slowly than controls. Limited evidence supports the view that damage from acidification does not necessarily result in lower reproductive yield^(4,5,7,10). Moreover, weak acidification from sulfate and nitrate compounds may stimulate yield by providing additional nutrients⁽⁵⁾.

In contrast, the increased mortality among seeds and seedlings exposed to extreme acidification is likely to alter both the floristic composition of the neighboring

vegetation and may also reduce genetic diversity. The results of SCHMALTZER *et al.*⁽²¹⁾ indicate that species composition changed dramatically over about 30 months after the first shuttle launch at John F. Kennedy Space Center in April 1981.

Moreover, the impact of launch emissions appears to be different on different growth forms. One third of trees and shrubs increased in relative cover while one third disappeared from their sites. One third of the grasses and sedges recorded after nine launches were not present on the sites after the first launch and over half of the herbs disappeared between the first and ninth launch. In general, the herbaceous flora was most sensitive and the grasses and sedges most resilient to near-field launch emissions⁽²¹⁾.

The apparent resilience of soil seed banks to a single SAD reported here requires further experimental work. It is possible that the germinable seed reserve in our small (100 g) soil samples was inadequate to detect significant changes in emergence after a single SAD. The mean number of seedlings that emerged was different in the four soils, and the Tangair soil in particular had high variance between replicates. Furthermore, several other factors, not included in the design of this experiment, will influence the number of seeds that germinate. Many species require heat, other chemical stimuli and specific environmental conditions to germinate⁽⁸⁾.

In order to better understand the direction of vegetation change after sequential exposures to emissions from shuttle launches we encourage the development of carefully designed field experiments complimented by experiments under controlled conditions. Of particular relevance is the interaction between the effects of shuttle emissions and other factors that limit seedling establishment in the field (e.g., moisture stress, herbivory). If we are to manage communities subject to chronic disturbances and stresses effectively, only careful experimentation will

allow the development of predictive models.

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REFERENCES

1. ADAMS C. M., DENGLER N. G. and HUTCHINSON T. C. (1984) Acid rain effects on foliar histology of Artemisia tilesii. Can. J. Bot. 62, 463-474.
2. COLE R. C., GARDNER R. A., GOWANS K. D., BEGG E. L. and HUNTINGTON G. L. (1958) Soil surveys of the Santa Barbara area, California. USDA, Soil Conservation Service, Washington D.C.
3. COULOMBE H. N. and MAHRDT C. R. (1976) (Eds) Ecological assessment of Vandenberg AFB, California. Volume II, Biological Inventory. Air Force Civil Engineering Center, Florida. AFCEC-TR-76-15.
4. EVANS L. S. and LEWIN K. F. (1981) Growth, development and yield responses of Pinto Beans and Soyabeans to hydrogen ion concentrations of simulated acid rain. Envir. Exp. Bot. 21, 103-113.
5. FUNK D. W. and BONDE E. K. (1986) Effects of artificial mist on growth and reproduction of two alpine plant species in the field. Amer. J. Bot. 73, 524-528.
6. HAINES B, STEFANI M. and HENDRIX F. (1980) Acid rain: threshold of leaf damage in eight plant species from a southern Appalachian forest succession. Water, Air and Soil Pollut. 14, 403-408.
7. JACOBSON J. S., OSMELOSKI J., YAMADA K. and HELLER L. (1987) The influence of simulated acidic rain on vegetative and reproductive tissues

- of cucumber (Cucumis sativus L.). New Phytol. 105, 139-147.
8. KEELEY J. E. (1987) Role of fire in seed germination of woody taxa in California chaparral. Ecology 68, 434-443.
 9. LEE J. J. and WEBER D. E. (1979) The effect of simulated acid rain on seedling emergence and growth of eleven woody species. For. Sci. 25, 393-398.
 10. LEE J. J., NEELY G. E., PERRIGAN S. C. and GROTHAUS L. C. (1981) Effects of simulated sulphuric acid rain on yield, growth and foliar injury of several crops. Envir. Exp. Bot. 21, 171-185.
 11. LERMAN S. (1976) The phytotoxicity of missile exhaust products: short term exposures of plants to HCl, HF and Al₂O₃. U.S. Department of Commerce, National technical Information service, AD-A026 837.
 12. MADSEN B. C. (1981) Acid rain at Kennedy Space Center, Florida: recent observations. Atmos. Envir. 15, 853-862.
 13. McCOLL J. G. and JOHNSON R. (1983) Effects of simulated acid rain on germination and early growth of Douglas-fir and ponderosa pine. Plant and Soil 74, 125-129.
 14. MIROV N. T. and KRAEBEL C. J. (1939) Collecting and handling seeds of wild plants. Civilian Conservation Corps, Forestry Publication No. 5.

15. MOORE R. P. (1962) Tetrazolium as a universally acceptable quality test of viable seed. Proc. Int. Seed Testing Ass. 27, 795-805.
16. MUNZ P. A. (1959) A California Flora. Univ. Calif. Press, Los Angeles.
17. PERCY K. (1983) Sensitivity of eastern Canadian forest tree species to simulated acid rain precipitation. Aquilo. Ser. Bot. 19, 41-49.
18. PERCY K. (1986) The effects of simulated acid rain on germinative capacity, growth and morphology of forest tree seedlings. New Phytol. 104, 473-484.
19. RAYNAL D. J., ROMAN J. R. and EICHENLAUB W. M. (1982) Response of tree seedlings to acid precipitation. I. Effect of substrate acidity on seed germination. Envir. Exp. Bot. 22, 377-383.
20. SCHERBATSKOY T., KLEIN R. M. and BADGER G. J. (1987) Germination responses of forest tree seed to acidity and metal ions. Envir. Exp. Bot. 27, 157-164.
21. SCHMALZER P. A., HINKLE C. R. and BREININGER D. (1985) Effects of space shuttle launches STS-1 through STS-9 on terrestrial vegetation of John F. Kennedy Space Center, Florida. NASA Technical Memorandum 83103.
22. SCHMALZER P. A., HINKLE C. R. and DRESCHER T. W. (1986) Far-field deposition from space shuttle launches at John F. Kennedy Space Center, Florida. NASA Technical Memorandum 83104.

23. SCHOPMEYER C. S. (1974) Seeds of woody plants in the United States.
USDA, Forest Service, Agriculture Handbook No. 450.
24. ZEDLER P. H. and MARION G. (1985) The effect of acid deposition on
potentially sensitive soil-plant systems. Annual report, AFOSR Grant No.
84-0284.

Table 1. Description and distribution of the species used in the experiments reported. Data are from MUNZ(16). C = California, E = introduced from Europe.

Species	Growth form	Habitat	Distribution
<u>Artemisia californica</u>	shrub	coastal sage (CS)	central-southern C
<u>Baccharis pilularis</u>	shrub	coastal sage	central C
<u>Bromus diandrus</u> (E)	annual grass	disturbed areas	southern C
<u>Coreopsis gigantea</u>	shrub	dunes and coastal scrub	central C
<u>Eschscholtzia californica</u>	annual/perennial	widespread	entire C
<u>Lotus scoparius</u>	sub-shrub	coastal sage-chaparral	entire C
<u>Lupinus arboreus</u>	shrub	strand, CS-pine forests	north-central C
<u>Mimulus aurantiacus</u>	sub-shrub	woodlands and scrub	north-central C
<u>Scrophularia californica</u>	perennial herb	forests and scrub	north-central C

Table 2. Mean soil pH (\pm SD; n = 12 pots) approximately 40 days after exposure to a single SAD (see Methods) to each of the four soil types in the vicinity of the launch facilities at Vandenberg Air Force Base.

SAD	Dune	Baywood	Tangair	Santa Lucia
0.5	2.56 \pm .43	2.52 \pm .38	2.46 \pm .29	2.28 \pm .10
1.5	3.30 \pm .21	3.99 \pm .16	3.98 \pm .25	3.94 \pm .28
2.5	4.20 \pm .14	5.56 \pm .21	5.37 \pm .23	5.05 \pm .18
5.6	4.81 \pm .18	6.21 \pm .23	5.92 \pm .13	5.36 \pm .16

Table 3. (a) Seedling survivorship and (b) pot yield (mg) for A. Californica, B. pilularis and M. aurantiacus grown for 30 days on four soils after exposure to a single SAD of pH 2.5 compared to controls at pH 5.6. Note that all seeds exposed to a single SAD of pH 0.5 or 1.0 died. Two-way ANOVA was performed on $\log(x+1)$ transformed values for each species. Mean values are given in Fig. 1. *** $P < .001$; * $P < .05$

(a) Seedling survivorship per pot 30 days after treatment

Source	df	<u>A. californica</u>		<u>B. pilularis</u>		<u>M. aurantiacus</u>	
		MS	F	MS	F	MS	F
Soil	3	0.750	60.70***	1.09	19.40***	0.150	4.40*
SAD	1	0.006	0.45	0.040	0.73	0.260	7.60*
S x SAD	3	0.037	2.99*	0.045	0.81	0.073	2.20
Error	24	0.012		0.056		0.034	

(b) Pot yield (mg) 30 days after treatment

Source	df	<u>A. californica</u>		<u>B. pilularis</u>		<u>M. aurantiacus</u>	
		MS	F	MS	F	MS	F
Soil	3	4.849	205.10***	3.028	24.50***	0.685	27.00***
SAD	1	0.282	11.90***	0.030	0.24	0.055	2.16
S x SAD	3	0.046	1.96	0.164	1.33	0.011	2.20
Error	24	0.024		0.124	0.025		

Table 4. The effect of seed moisture and simulated acid deposition (SAD) on percent germination, compared by two-way analysis of variance of arc-sine transformed proportions of germinated seeds. Germination response was recorded on the soil type which supported the species at the study sites. Untransformed means for each level of each factor are given in Table 5. Soil are: D = Dune; B = Baywood; T = Tangair; S = Santa Lucia.

Species	Soil type	Sources of variance						Error MS
		Seed moisture		SAD		Interaction		
		MS	F _{1,18}	MS	F _{2,18}	MS	F _{2,18}	
<u>Coreopsis gigantea</u>	D	.039	3.58	.460	41.99***	.004	0.39	.011
<u>Lupinus arboreus</u>	SL	.168	2.08	1.100	13.6***	.084	0.52	1.45
<u>Eschscholtzia californica</u>	B	.033	1.10	.102	3.38*	.070	1.16	.035
<u>Scrophularia californica</u>	B	.009	0.28	.014	0.45	.022	0.69	.032
<u>Artemisia californica</u>	D	.205	8.35***	1.391	56.13***	.178	7.24***	.443
<u>Artemisia californica</u>	B	.033	2.16	.890	58.11***	.118	7.68***	.015
<u>Artemisia californica</u>	T	.019	2.38	.456	58.08***	.041	5.22*	.008
<u>Artemisia californica</u>	SL	.013	0.28	1.563	34.97***	.012	0.27	.045
<u>Lotus scoparius</u>	B	.034	9.04***	.049	12.92***	.009	2.37	.004
<u>Bromus diandrus</u>	B	.171	35.30***	.074	15.34***	.021	4.37*	.005
<u>Bromus diandrus</u> [#]	SL		not tested	1.07	5.15*			.114

[#] No dry treatment tested, df = 1,11.

Table 5. Germination of seeds exposed to a single SAD. Seeds were either air-dry or had imbibed water for 24 hours. Data are the mean proportion germinating (\pm SD) from four replicates (see Methods). Soils are: D = Dune; B = Baywood; T = Tangair; and SL = Santa Lucia.

Species	Soil type	Dry seeds			Imbibed seeds		
		pH 1.0	pH 2.0	pH 5.6	pH 1.0	pH 2.0	pH 5.6
<u>Coreopsis gigantea</u>	D	.27 \pm .08	.65 \pm .12	.67 \pm .11	.20 \pm .08	.53 \pm .09	.64 \pm .09
<u>Lupinus arboreus</u>	SL	.14 \pm .13	.40 \pm .20	.50 \pm .12	.25 \pm .09	.48 \pm .07	.51 \pm .11
<u>Eschscholtzia californica</u>	B	.61 \pm .14	.84 \pm .17	.85 \pm .11	.68 \pm .16	.76 \pm .09	.75 \pm .10
<u>Scrophularia californica</u>	B	.88 \pm .09	.96 \pm .06	.95 \pm .08	.93 \pm .07	.92 \pm .11	.93 \pm .04
<u>Artemisia californica</u>	D	.11 \pm .17	.47 \pm .15	.66 \pm .12	.02 \pm .02	.07 \pm .04	.75 \pm .11
<u>Artemisia californica</u>	B	.03 \pm .04	.66 \pm .08	.50 \pm .19	.08 \pm .05	.34 \pm .05	.46 \pm .12
<u>Artemisia californica</u>	T	.59 \pm .11	.85 \pm .08	.83 \pm .05	.38 \pm .10	.90 \pm .04	.82 \pm .02
<u>Artemisia californica</u>	SL	.20 \pm .27	.88 \pm .06	.86 \pm .12	.19 \pm .19	.79 \pm .16	.82 \pm .05
<u>Lotus scoparius</u>	B	.46 \pm .07	.60 \pm .03	.66 \pm .10	.46 \pm .03	.47 \pm .04	.56 \pm .05
<u>Bromus diandrus</u>	SL	no treatment on dry soil			1.0 \pm .0	.99 \pm .02	
<u>Bromus diandrus</u>	B	.98 \pm .02	1.0 \pm 0.0	1.0 \pm 0.0	.89 \pm .04	.95 \pm .02	.99 \pm .02

Table 6. The effect of each level of the SAD treatment on arc-sine transformed proportions of germinated Artemisia californica seeds found on four soil types under imbibed and dry seed condition, compared by separate two-way ANOVA. Untransformed means for each level of each factor are given in Table 4. *** $P < .001$; * $P < .05$

Source	df	Levels of SAD					
		pH 1.0		pH 2.0		pH 5.6	
		MS	F	MS	F	MS	F
Seed moisture	1	.017	.41	.383	28.50***	.0003	.02
Soil type	3	.606	14.80***	.909	67.50***	.271	18.10***
Interaction	3	.059	1.44	.119	8.87***	.011	.73
Error	24	.041		.013		.015	

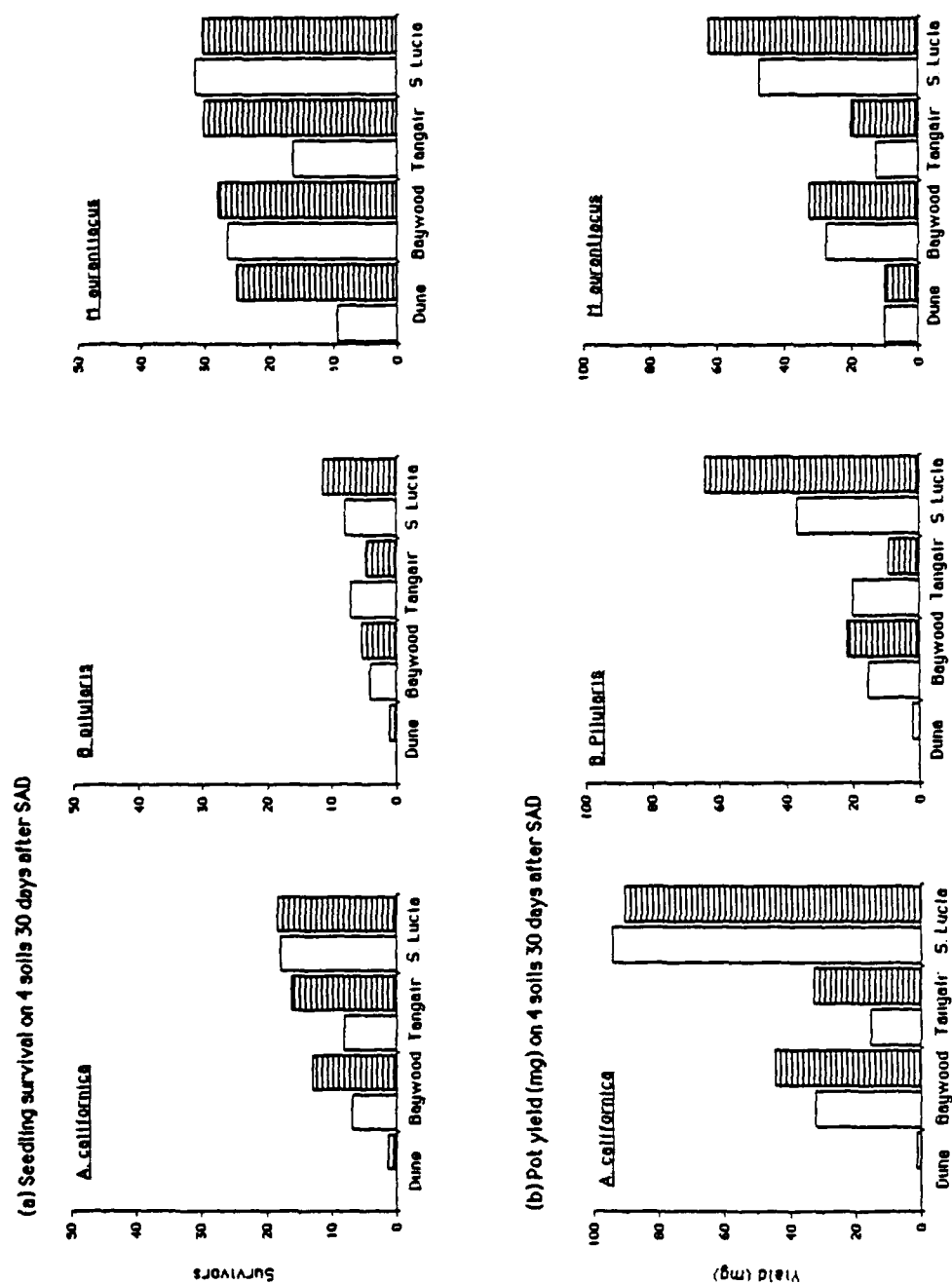


Fig. 1. Comparison of (a) the mean number of surviving seedlings ($n = 50$) and, (b) mean pot yield (mg) 30 days after exposure to a single SAD. The SAD treatment had two levels; pH 2.5 (clear bars) and control of pH 5.6 (horizontal bars). Each of the three species was grown on four soils.

PART 3

INFLUENCE OF EXTREME ACID DEPOSITION ON COMPETITIVE
INTERACTIONS BETWEEN PINUS MURICATA AND ARTEMISIA
CALIFORNICA

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Three replacement series experiments were done which investigated the performance of two species from Vandenberg AFB growing on native soils in pure and mixed culture under various treatments. One experiment involved the response of the species to drought while the other two experiments involved the response of the species to different modes of acid deposition. The purpose of these competition experiments was to determine if acid depositions of the magnitude derived from shuttle launches could potentially alter the interactions between species.

Soils and Species

Pinus muricata D. Don. (Bishop pine) and Artemisia californica Less. (Coastal sagebrush) were selected for the following experiments for several reasons. First, both species occur locally in the Vandenberg area and they are distributed on similar soil types. Second, distinct boundaries exist between these species as the gradient between the sandy coastal terrace soils give way to the shale derived soils away from the immediate coast. Third, characteristics of species (e.g. foliar damage, changes in abundance) and the properties of soils (soil pH, nutrient status) can be altered by extreme inputs of acid deposition such as those generated by the launching of space vehicles. How interactions between these two species might be effected by changes in species characteristics and soil properties caused by increased deposition of acid fallout from the launching of space shuttles in the vicinity were of interest and set the scene for the experiments.

Examples of where boundaries between the two species can occur are on the Santa Lucia and Tangair soils. The Santa Lucia soil is a well drained, slightly acidic, shaly clay loam over a siliceous shale bedrock distributed on moderate to steep slopes generally inland and at higher elevations than the soils making up the coastal

terraces (USDA 1972). The Tangair soil is a somewhat poorly drained, slightly acidic, sandy soil which contains small iron concretions in the subsoil (USDA 1972). This soil type is derived from old marine deposits overlying shale on the coastal terraces and in Santa Barbara County the Tangair series is almost entirely contained within the boundaries of Vandenberg Air Force Base.

Pinus muricata is a relatively small, slender, two needle pine which occurs on Santa Cruz Island and along the coast from Santa Barbara County to Humboldt County, California (Smith 1976). In Santa Barbara County, in particular at Vandenberg Air Force Base (VAFB), localized stands of this species can be found on both Santa Lucia and Tangair soil types (Coulombe and Mahrtdt 1976). A serotinal species in this part of its range (Duffield 1951), P. muricata retains most of the seed bank within closed cones in the canopy. Seed release followed by large pulses of seedling establishment occur only after fire. However in other areas, P. muricata is less serotinous (Duffield 1951) and seedling establishment may occur during the long interval between fires.

Artemisia californica is a widely distributed grayish aromatic shrub. It occurs along the coast and low inland fans from lower California to central California and also on the major offshore islands (Smith 1976). One of the major component shrub species of the coastal sage scrub in the Vandenberg region this shrub grows well on both Santa Lucia and Tangair soils and it may dominate local areas along the coast (Coulombe and Marhdt 1976). A. californica has a weak ability to resprout after fire, and can easily establish seedlings both between and after fires (Malanson and Westman 1985). It disperses seeds annually but probably has no long term soil seed reserve.

Acid treatment experiments

The repeated deposition of acid solutions of high concentrations, such as those generated by shuttle launches, can have effects on the species composition of plant communities, have detrimental effects on foliar tissues, and result in changes in soil properties (Granett 1983; Hinkle et. al. 1986; Schmalzer 1985,1986). In this study, two experiments were designed to investigate the effects of acid deposition on the performance (competitive interaction) between Artemisia californica and Pinus muricata seedlings when grown on native soils in pure and mixed cultures. The first experiment involved a single application of pH 1.0 hydrochloric acid (HCl) to the foliage of three month old seedlings of each species. A second experiment involved the repeated treatment of native soils with HCl solutions of varying pH and then measuring the performance of each species when grown on these treated soils.

EXPERIMENT 1: THE EFFECT OF A SINGLE FOLIAR APPLICATION OF PH 1.0 HYDROCHLORIC ACID ON GROWTH, BIOMASS PRODUCTION AND RELATIVE YIELD OF PINUS MURCATA and ARTEMISIA CALIFORNICA GROWING IN PURE AND MIXED CULTURE.

The effects acidic rain has on plant foliar tissues are well documented. In general, the type of acid, pH of the rain, the magnitude and duration of exposure, and the plant species involved are all factors determining the amount and kind of damage to plant tissues (State University of New York 1982, 1984; Evans and Curry 1979). These effects can be superficial (e.g. erosion of the cutin layer), or they can lead to the death and abscission of plant parts (Evans et al. 1977; Percy and Baker 1987; Tamm and Cowling 1977; Temple 1987). The extent of foliar damage tends to increase with leaf area (Evans et. al. 1977) and increasing acidity (Haines et. al. 1980). Foliar

nutrients (K^+ , Ca^{++} , amino acids, proteins) can also be leached (Scherbatskoy and Klein 1983).

The bulk of the research on the effects of foliar deposition of acid on plant tissues deals with rain acidified by nitrogen and sulfur emissions. These sources of pollutants and the resulting acids are different from the kinds of emissions which come from the launching of space rockets. In particular, the solid rocket boosters used to launch the space shuttle emit vast amounts of chloride gas and aluminum particulates. The chloride gas reacts with water (used to cool the launch pad and dampen sound) to form hydrochloric acid which can have a pH of 0.5 near the launch complex (Anderson and Keller 1983).

Experiments designed to determine the effects of hydrogen chloride gas on plant tissues show that significant leaf damage does occur when plants were exposed to high concentrations of HCl gas and that the amount of damage was dependent on the exposure duration, plant species, and tissue age (Lind and London 1971; Lerman et. al. 1976; Endress et. al. 1978, 1979; Granett and Taylor 1981). Studies of the effect of HCl deposition on vegetation around launch areas have been done at John F. Kennedy Space Center, Florida, in conjunction with shuttle launches there. These studies showed that near field effects on vegetation can be quite severe, far-field effects on vegetation are dependent on the concentration of HCl deposition and plant sensitivity, and that the recovery of the vegetation in both areas is dependent on the frequency of launches (Schmalzer et. al. 1985, 1986). Pre-launch studies in the Vandenberg area report that the economic plant industries in the region may be significantly affected if "launch clouds" reach nearby agricultural fields (Granett 1983). A pre-launch study on the effects of acid deposition on native vegetation in the Vandenberg area show that extreme doses of acid (pH .05-1.0 HCl) can inhibit germination and establishment of species native to the Vandenberg area while

acidities in the range of pH 2.5-5.6 may reduce or stimulate germination depending on the species and soil type (Zammit and Zedler 1988).

This experiment was designed to determine how a single application of HCl of extreme pH (1.0) might affect the competitive abilities of the native species Artemisia californica and Pinus muricata during the establishment phase of their life cycles. The growth, biomass, and relative yield of seedlings of these two species were used as measures of performance. The hypothesis tested was that Artemisia californica, a broadleaf species, is more sensitive to foliar applications of acid than Pinus muricata, a coniferous species.

METHODS

Planting

Seeds of A. californica and P. muricata were germinated in growth chambers. Pairs of seedlings were planted in two planting mixtures in 250 cc. pots containing Tangair soil collected at VAFB. Pure cultures contained either two Pinus or two Artemisia seedlings while mixed cultures contained one seedling of each species. The seedlings were allowed to grow in a covered greenhouse for three months (March-June 1987) before treatments were applied.

Acid Treatments

After 3 months growth, the pots in each planting mixture were randomly assigned an application treatment so that there were 10 replicates (pots) per mixture per treatment (Table1). Treatments were applied once using an atomizer spray bottle and the rate of deposition was on a per area basis. Half the pots were sprayed with 1.8 ml of pH 1.0 HCl and the other half with an equal amount of de-ionized water to act

as a control. The amount of acid applied was calculated from reported rates of near field deposition (6.7 g HCl/m^2 or $183 \text{ meq H}^+/\text{m}^2$) from several shuttle launches at Kennedy Space Center (Milligan and Hubbard 1983, Marion et. al., this report). After treatment, the seedlings were grown for one month and then harvested.

Measurements and Analysis

Growth throughout the experiment was estimated by calculating the change in height of the seedlings from monthly height measurements. Final plant heights were measured prior to harvesting 1 month after the foliar application of treatments. Harvested plants were used to estimate total biomass production which was divided into a shoot and root portion. Root:shoot ratios and relative yields were also calculated. A three-way ANOVA was used to determine statistical differences between the main effects species (*A. californica*; *P. muricata*), planting mixture (pure; mixed), and spray treatment (acid; water) along with any interactions.

RESULTS

Productivity

The relationship between species, growing mixture, and the effect of a single foliar application of pH 1.0 HCl proved to be complex and interactive (Table 2). This was especially true for height change after treatment, shoot biomass, and total biomass. Analysis of root biomass and root:shoot ratios were more easy to interpret. Several general trends can, however, be suggested by observing the distribution of the mean values (Table 3).

The growth of both species, expressed as the change in height, was retarded after the application of a single dose of pH 1.0 HCl when compared to those treated with de-

ionized water (Table 3). This was especially true for Artemisia seedlings grown in mixed culture.

Seedlings of Pinus had greater total biomass (dry weight), overall, than Artemisia seedlings (Table 3). This is reflected in greater shoot and root biomass accumulations for the Pinus seedlings. For Artemisia seedlings, there was more total biomass for the acid treated seedlings than the controls and this is probably a direct effect of the larger accumulation of shoot biomass observed for these seedlings. It appears that there was a stimulation in shoot biomass production for Artemisia in pure and mixed culture after acid treatment.

The root:shoot ratios tended to be higher, though not significantly, in the control treatments than in the acid treatment for both species across all mixtures (Table 3). There was, however, a significant difference in root:shoot ratios between mixtures overall, with plants grown in pure culture having larger ratios (a greater proportion of roots to shoots). This may indicate an interaction between species for rooting space in the mixed cultures.

Relative yield

In order to make an assessment of the magnitude and direction of the competitive interactions, if any, between the two species, relative yields were calculated for two of the measures of performance; final height and total biomass. These relative yield values were calculated by dividing the mean of the measure of performance for the mixed culture by the mean of the same factor for the pure culture within each species. When plotted on a graph the direction of the competitive interactions are determined by which quadrant of the relative yield graph the calculated values lie while the magnitude of the interaction is determined by how far within the

quadrant the value lies with respect to the intersection of the relative yield equals 1 line (Figure 1; Harper 1977).

For this experiment, the two relative yield graphs suggest that the species are interacting, but that this does not have a strong competitive element. Acid application changes the nature of the interaction. Considering height, both species do better in the presence of the other in the control, but when acid is applied this apparent synergistic effect is cancelled, with Pinus performing about the same in mixed and pure cultures and Artemisia performing more poorly (Figure 2). The biomass data likewise show that acid shifts the interaction, in this case from Pinus neutral and Artemisia depressed to Pinus appearing to be suppressed by Artemisia (Figure 3).

DISCUSSION

Detecting competition between species remains a controversial topic because of methodological difficulties and because interpretation of analyses is rarely clearcut (Connolly 1986,1987; Firbank and Watkinson 1987; Mead 1979; Snaydon 1979; Sih et. al. 1985). In their reviews of field experiments designed to investigate competition, both Connell (1983) and Schoener (1983) found a high percentage of studies demonstrating competition. Despite this evidence, they conclude that it is still difficult to produce clear demonstrations of interspecific competition in field situations. However, insights into the nature of interactions between species grown with themselves and with other species can be drawn from simple experiments which measure the performance of these species growing in various mixtures (Heywood and Levin 1986; Davidson and Robson 1986; Armstrong 1985; Shainsky and Radosevich 1986). The results of these performance tests, although often statistically complex, suggest that interactions between species exist, but whether

these interactions can be called truly "competitive" in nature is highly debatable. Performance in these experiments referred to relative yields, relative growth rates, physiological measures, or biomass allocation. Performance, as used in the set of experiments reported on here, was measured by differences in productivity (growth and biomass) and relative yields of the two species in response to different soils and varying treatments.

A single application of pH 1.0 HCl was sufficient enough to retard the growth (change in height) of three month old Pinus and Artemisia seedlings. Final height relative yield results suggest that Artemisia was the more sensitive of the two species to acid treatment. This greater sensitivity may be due to the more delicate herbaceous tissue Artemisia possesses in comparison to the more sclerophyllous tissue of a pine needle. Although conifer foliage has been suggested to be more resistant to acid deposition than broadleaf species (Lee and Weber 1979; Maurice and Crang 1986; Percy 1986) damage to conifer needles can be highly variable, occurring in some instances (Wood and Borman 1977, McColl and Johnson 1983, Armentano et. al. 1987) while not in others (Maurice and Crang 1986; McColl and Firestone 1987).

The greater yield of the Pinus seedlings across all mixes and treatments may be explained by the greater proportion of heavier woody stem tissue. What is noteworthy is the apparent stimulation of shoot biomass production for the acid treated seedlings of Artemisia. This is because the lateral buds were released due to the death or damage of the apical meristem by the acid. The biomass increase may thus be a consequence of the early recruitment of lateral stems on these seedlings. Jacobson et. al. (1987) found a similar capacity to recover and compensate for damage to foliage due to acid application in cucumbers (*Cucumis sativus* L.) while Lee et. al. (1981) found a stimulation in the stems and leaves of sweet corn. The magnitude of

the competitive advantage for Artemisia may be an indirect measure of this shoot stimulation. The effect of foliar applications of acid on the yield of plants in general is, however, highly variable. Studies performed on crop plants exposed to foliar applications of acid indicate that significant reductions in yield depend on the species, exposure, and acidity of the rain (Lee et. al. 1981; Evans et. al. 1986; Ashendon and Bell 1987; Temple et. al. 1987; and Olson et. al. 1987). The yield of some crop species appear unaffected by foliar applications of acid (Lee et. al. 1981; Pell et. al. 1987; and Jacobson et. al. 1987).

This experiment provides evidence that a single foliar application of extreme acidity is enough to shift the interaction between seedlings of Artemisia californica and Pinus muricata despite the initial foliar damage to Artemisia. The explanation for this complex pattern appears to lie in the different way that the two species react to acid deposition. Artemisia foliage is sensitive to acid but is able to sprout from dormant buds. Thus height is negatively affected, but biomass production is apparently stimulated. Whether the advantage gained by Artemisia at this stage of the life cycle would continue into later stages is dependent on the long term ability of both species to recover. Also, as in the case of shuttle launches, the ability of the species to recover from repeated acid deposition events could make a substantial difference in the magnitude of the shifts in the interactions.

EXPERIMENT 2: THE EFFECT OF ACID-LEACHED SOILS ON THE GROWTH, BIOMASS PRODUCTION AND RELATIVE YIELD OF PINUS MURCATA and ARTEMISIA CALIFORNICA SEEDLINGS.

The effects acid deposition has on soils are complex due to the nature of the interactions between soil physical and chemical properties. There are, however, some generalizations that have emerged from the studies of acid inputs to soil systems. Soil sensitivity ratings have been developed that rate soils on their resistance to change from acid deposition. Early rating systems were based on buffering capacity and base saturation of soils (Wiklander 1980; Bache 1980; Peterson 1980). The latest rating systems rely more on cation exchange capacities and soil pH to assess sensitivity to change by acid inputs (McFee 1983; Reuss and Johnson 1986). Depending on the system used, the most sensitive soils appear to be noncalcareous sandy soils with pH > 5.0 (Wiklander 1980), shallow poorly buffered sandy textured soils also low in organic matter (Bache 1980), soils with low cation exchange capacities and pH > 5.0 (McFee 1983), and soils having moderate to high base saturation but low cation exchange capacities (Reuss and Johnson 1986).

It is widely accepted that the continued deposition of relatively low pH acid solutions on soils will increase the leaching of base cations (e.g. Ca^{++} , Mg^{++}) and may increase the mobility of Al^{+++} ions resulting in alterations to the buffering capacity of the soil and a lowering of the soil pH (Baker and Hocking 1977; Johnson et. al. 1982; Hinkle et. al. 1986; Reuss and Johnson 1986, Marion et. al., this report). The rate of base cation leaching is dependent on the size of the pool of exchangeable bases, the rate of replenishment by weathering, the level of acid deposition, and the amount of mobile anions present (Johnson et. al. 1982; Reuss and Johnson 1986).

Leached cations may become immobilized and accumulate in soil horizons 25 cm to 100 cm deep in some soils (Kelly and Strickland 1987).

Major plant nutrients such as phosphorous and nitrogen may also be affected, but not always in a straightforward manner (Aber et. al. 1982). Cole and Stewart (1983) suggest that as soils become acidified the amount of phosphorous in soil solution and organic forms should increase. These increased phosphorous levels are due to chemical weathering and decreases in microbial turnover, respectively. Nitrogen losses are commonly from the leaching of nitrate (NO_3), a highly mobile anion, while ammonia (NH_4) is more resistant to leaching due to binding within the exchange complex (Johnson et. al. 1982; Reuss and Johnson 1986; Kelly and Strickland 1987). The lowering of the soil pH due to acid inputs can do several things. First it may inhibit the oxidation of NH_4 to NO_3 . Second, it can cause a decrease in organic matter decomposition which reduces the amount of available nitrogen. Third, soil acidification can increase the leaching of nitrates (NO_3) which ultimately depletes base cations decreasing the soil pH further (Aber et. al. 1982; Reuss and Johnson 1986). Although nitrogen mineralization can be inhibited and NO_3 production lowered with acid treatments, Stroo and Alexander (1986) report that this condition occurs immediately after treatment and that with acid free intervals soils may have a rapid recovery of N-mineralization.

Changes in soil chemical properties as well as changes in soil pH will usually take place only after long periods of continued exposure with acid depositions of pH 4.0 or less (Reuss 1980; Reuss and Johnson 1986). This process may be accelerated, however, as in the case of repeated depositions of concentrated acid solutions like those characteristic near space shuttle launch areas (Hinkle et. al. 1986).

The purpose of this experiment was to determine the effect of soils leached repeatedly with acid solutions of varying pH on the competitive interactions between seedlings of two native species of the Vandenberg area, Artemisia californica and Pinus muricata. This was an attempt to simulate a series of closely spaced shuttle launches at various distances from the launch site. Performance of the two species was determined by using growth and biomass measurements and competitive effects judged by the use of relative yields. The hypothesis tested was that Pinus muricata seedlings are more tolerant of acid treated soils than Artemisia californica seedlings and thus gain a competitive advantage in growth, biomass, and relative yield as the pH of the soil decreases.

METHODS

Preparation of Soils

Representative samples of Santa Lucia and Tangair soils were collected from VAFB, air dried, and passed through a 2mm. sieve to remove the larger stones. The total volume of each soil type for each treatment level was estimated and divided into 5 equal parts which were placed into large tubs. Soils in these tubs were leached on a soil volume/acid volume basis with dilutions of 1N hydrochloric acid by adding 1.6 ml HCl of the adjusted pH per cc. of soil. This was equivalent to near field deposition rates as recorded for shuttle launches at Kennedy Space Center of 6.7 g HCl/m² (183 meq H⁺/m²) of soil (Milligan and Hubbard 1983; Marion et. al., this report) to a depth of 20 cm.. Thus, 20.4 ml of hydrochloric acid; either pH 1.0, 2.5, or 5.6 (ambient), was added to the appropriate replicate tub. The soils were thoroughly mixed to assure dispersion of the acid throughout the tub and were left to stand for 24 hours. Each tub of soil was then leached with 400 ml of de-ionized water. This was equivalent to 2.7 cm of water (soil volume/rain volume) which was an

approximation of the mean monthly rainfall for the Vandenberg area. The leachate was collected, the pH measured, and the samples were stored for later nutrient analysis. The tubs were left to drain for 2 days and the above procedure was repeated five times. After the last treatment, the soils were allowed to dry and the tubs of soil within treatments and soil type were combined and placed into 250 cc pots.

Planting

Seeds of both species were germinated in growth chambers to assure uniform seedling size and numbers at the time of planting. Seedlings were planted two to a pot in two mixtures. The pure culture pots contained two seedlings of either Pinus or Artemisia while the mixed culture pots contained one seedling of each species. Each planting mixture and the three pH treatment levels were replicated 16 times within soil types (Table 4). The plants were watered regularly and allowed to grow for three months (March- June 1987) in a covered greenhouse.

Measurements

Growth of the seedlings was monitored by calculating the change in height of the seedlings from monthly height measurements. A final height measurement was taken immediately before the seedlings were harvested after 3 months growth. Total biomass was estimated from oven dried plants and was partitioned into a shoot and root portion. Root:shoot ratios were also determined. Relative yields were calculated by dividing the mean yield in the mixture by the mean yield in pure culture for the respective performance measure. The soil in the pots was allowed to dry after harvesting the plants and the soil pH was measured from a 1:1 paste of water to soil using a pH probe. The leachates collected during the acid leaching process were analyzed for nitrate, ammonia, and phosphate using standard techniques (Technicon 1987a,b,c). Foliar nutrients (phosphorous and total Kjeldahl nitrogen)

were determined by analyzing the acid digests of leaves or needles of each species (Technicon 1987d). All nutrients were measured using a Technicon Autoanalyzer II.

RESULTS

Soil pH

The results for the effect of pH treatment on the soil pH of the two native soils indicate a significant interaction between soil type and pH treatment (Table 5). An examination of the means for each treatment and soil type show a soil pH difference between the two soils with the Santa Lucia soil having the more acidic soil pH across all treatments (Table 6). The rate of decrease in soil pH as the treatments became more acidic appears greater for the Santa Lucia soil and the largest change in soil pH occurred when either soil was treated with pH 1.0 HCl solution.

Leachate Analysis

pH- The pH of the soil leachate was affected by pH treatment, soil type, number of treatments, and strong interactions among these factors (Table 7). Examination of the means reveals the source of the interactions (Table 8). The general trend suggested was that the leachate pH declined more or less continuously at pH 1.0 in both soil types while the leachate pH showed little change as the number of leachings increased for the pH 2.5 and 5.6 treatments. In addition, the leachate from Santa Lucia soil appeared more sensitive to changes in pH at the pH 1.0 treatment than the Tangair soil similarly treated.

Nutrients

Nitrate: After five leachings with HCl of varying pH, the Santa Lucia soil had a significantly greater total release of nitrate than the Tangair soil (Table 9). However,

the total amount of nitrate released was consistent between pH treatments within soil types (Table 10). These trends can be seen more clearly when the cumulative loss of nitrate for the two soils and three treatments is graphed against the number of leachings (Figure 4a). Although the same amount of nitrate is released by the two soils for all treatments initially, the rate of release was greater for the Santa Lucia soil as the number of leachings increased across all treatments.

Ammonia: There was a significant difference between soil types for the loss of ammonia (Table 9) such that the total ammonia leached was greater for the Tangair soil than the Santa Lucia soil (Table 10). It can be seen that this difference was strongly driven by the greater rate of release of ammonia at the pH 1.0 treatment on the Tangair soil by observing the cumulative loss of ammonia as a function of the number of leachings (Figure 4b). The total release of ammonia was not different for the different pH treatments on either soil due to the high variability of the means.

Phosphate: There was no effect of pH treatment or a difference between soil types for the total amount of phosphate released (Table 9). Approximately equal amounts of phosphate were released within soils between treatments and between soils overall (Table 10). Cumulative loss of phosphate by soil type and treatment (Figure 4c) reveals that although the largest amount of phosphate was released from Tangair soil treated with pH 1.0 solutions, the rate and amount of change between soils and treatments, overall, is approximately the same.

Plant productivity

Statistical analysis of the productivity factors revealed that the relationships between height change and biomass for the two species on the acid treated soils was complex and extremely interactive (Tables 11). Insights into this complex relationship can be inferred by examining the distribution of the mean values across the factors for all

treatments (Table 12). Germinated Artemisia seeds in pure culture on Santa Lucia soil leached with a solution of pH 1.0 HCl failed to grow. Survival and growth of Artemisia seedlings was low on Santa Lucia soil for the mixed culture (1 plant) and on Tangair soil for both mixtures (1 plant in pure, 5 plants in mixed) at the pH 1.0 treatments. This may be due to the lowering of the soil pH caused by the acid leaching process and the sensitivity of young seedlings of this species (Table 6).

In general, Pinus seedlings had greater final heights than Artemisia seedlings on the acid treated soils (Tables 11-12). There was a tendency, although not a significant one, for both species to grow taller in mixed culture. This was especially true for Artemisia seedlings growing on Santa Lucia soil. The effect of the acid treatments on final height was only strongly evident for Artemisia seedlings at the pH 1.0 level on Santa Lucia soil.

Total biomass accumulation for Artemisia seedlings tended to be larger when grown in mixed culture for both soil types and it was greatest when grown on the pH 5.6 treated Santa Lucia soil (Table 11-12). The large root production by Artemisia seedlings for this treatment may be the reason (Table 12). Total biomass of Pinus seedlings was essentially indifferent to mixture for both soils but did better than Artemisia overall on the Tangair soil. This result was due in part to the larger shoot biomass accumulation for Pinus on Tangair soil (Table 12). The effect of pH treatment was again only strongly evident for Artemisia seedlings at the pH 1.0 treatment on Santa Lucia soil for total biomass as well as individual root and shoot biomass.

Root:shoot ratios, in general, were greater for Artemisia seedlings than Pinus seedlings across both soils and all treatments (Table 11-12). This was most evident

for the Tangair soils where Artemisia seedlings produced a greater proportion of roots to shoots.

Relative yield

Relative yield comparisons were made for the final height and total biomass for the seedlings of both soils and the various acid treatments. These data show that the competitive effects of Artemisia on Pinus were extremely weak. Final height relative yield data show no strong effect on Pinus and only a weak negative effect on Artemisia seedlings growing on pH 2.5 treated Tangair soil (Figure 5). An indirect competitive advantage was gained by Pinus seedlings on pH 1.0 treated Santa Lucia soil due to the failure of growth of Artemisia seedlings. The biomass relative yield data hint at a slight advantage for Artemisia in the pH 5.6 treatments on both soils while the pH 2.5 treated Tangair soil had a weak negative effect on both species (Figure 6). The pH 1.0 treated Tangair soil had a slight positive effect on both species especially on Artemisia biomass while the failure of Artemisia seedlings to grow on the similarly treated Santa Lucia soils gave an indirect advantage to Pinus.

Foliar Nutrient Analysis

Nitrogen

Interactions between species, mixture, pH treatment, and soil type had significant effects on the concentration of nitrogen in the foliage of Pinus and Artemisia seedlings (Table 13). However, small sample sizes for Artemisia make drawing conclusions about the effect of pH 1.0 treatments on foliar nitrogen concentrations for this species difficult and it may make the significance patterns detected less reliable.

Although the results are complex several patterns emerged from the distribution of the mean values (Table 14). Overall, Artemisia seedlings had greater concentrations of nitrogen in their foliage. Within species, foliar nitrogen tended to be greater in pure culture in the pH 1.0 and 2.5 treatments and greater in mixed culture at pH 5.6 for Artemisia. Pinus seedlings tended to have greater foliar concentrations in mixed culture across all treatments. It appears that pH treatment played only a minor role in determining the foliar concentration of nitrogen for both species.

Total nitrogen content for foliage of Artemisia and Pinus seedlings was significantly influenced by interactions between species/mixture and species/pH treatment (Table 15). The only clear pattern revealed by examining the distribution of the mean values was a tendency for Artemisia growing in mixed culture on Tangair soil to have greater foliar nitrogen contents than those growing in pure culture on this soil (Table 16).

Phosphorous

There was a significant difference between species for the foliar concentration of phosphorous (Table 13). Overall, concentrations of phosphorous were greater in the foliage of Artemisia seedlings than Pinus seedlings (Table 14). Soil type, pH treatment, and planting mixture appear to have had little effect on the foliar concentration of phosphorous. Species, soil type, and planting mixture interactively affect the total content of foliar phosphorous in these species (Table 15), but other than the tendency for Artemisia seedlings in mixed culture on Tangair soil to have greater foliar phosphorous contents, no clear patterns were revealed (Table 16).

DISCUSSION

Repeated applications of pH 1.0 HCl and leaching with water decreased the soil pH of both Santa Lucia and Tangair soils more than applications of pH 2.5 or 5.6 HCl. Santa Lucia soils had a lower pH than Tangair soils across all treatments. These results are the opposite of predictions usually made about soils with these properties (Marion et. al., this report) and sensitivity ratings. Santa Lucia soils loams with moderate to high cation exchange capacity (68.6 meq./100 gm soil), soil pH of 5.9, and a reasonable base saturation (63%) (USDA 1972). According to guidelines for rating soils by Ruess and Johnson (1986), soils with ample cation exchange and base saturation coupled with a pH above 5.0 are resistant to change by acid inputs. Also, Santa Lucia soils are Mollisols, and Peterson (1980) suggests that soils of this order are typically not sensitive to acid inputs. Tangair soils are Entisols with a loamy sand texture, a low cation exchange capacity (6.0 meq./100 gm soil), soil pH of 6.2, and good base saturation (71%) (USDA 1972). Soils having moderate to high base saturation but a low cation exchange capacity are the most sensitive to change by acid inputs (Ruess and Johnson 1986) and Entisols, in general, are also rated as sensitive to change (Peterson 1980). Our results showed that the Santa Lucia soils were more sensitive to change by acid deposition than the Tangair soils.

One explanation of the differences observed between the two soils may be found in the amounts and kinds of nutrients leached from them. As discussed, the leaching of base cations from soils can alter buffering capacities and thus affect soil pH. It is also known that base cation leaching can be enhanced by the presence of highly mobile anions (Reuss and Johnson 1986). Santa Lucia soils tend to have higher total nitrogen contents than Tangair soils (Marion et. al., this report) and thus, theoretically, might contain greater amounts of nitrate, a highly mobile anion. Our results showed that the Santa Lucia soils had significantly greater losses of nitrate

over Tangair soils. Consequently, this increased loss of nitrate may have depleted the base cations more rapidly in the Santa Lucia soil decreasing the soil pH at a higher rate than the Tangair soil. Ruess and Johnson (1986) support this hypothesis when they state that low nitrogen soils are more resistant to rapid changes in soil pH because of lower rates of nitrate leaching. Also, Scheir (1986) showed that the pH of the irrigating solution used on soils affected the pH and chemistry of collected leachate more at the lower pH treatments (3.0). He found that as the pH of the leachate decreased the amount of cations leached increased and the soil pH decreased.

The reduction in soil pH for both soils after acid treatments of pH 1.0 indicate that very young Artemisia californica seedlings are more sensitive to lower soil pH than young Pinus muricata seedlings. The effect acid deposition has on germination shows that species differ in sensitivity and degree of inhibition (Abrahamsen et. al. 1977; Raynal et. al. 1982; and Scherbatskoy et. al. 1987). Other studies suggest that germinative capacity is not as sensitive to acid deposition as is seedling survival (Lee and Weber 1979; McColl and Johnson 1983; Percy 1986). Our results showed that germinated Artemisia seeds either failed to emerge or had reduced seedling survivorship on Santa Lucia and Tangair soils treated with pH 1.0 HCl. This agrees with findings from Zammit and Zedler (1988) who showed that Artemisia establishment was prevented after a single dose of pH .05 or 1.0 HCl on Santa Lucia and Tangair soils. They also showed that germination of Artemisia was reduced more at pH 1.0 on Santa Lucia soil than on Tangair soil.

Soil acidification may reduce plant growth (Wood and Borman 1977; Percy 1986), stimulate plant growth (Scheir 1986; Reich et. al. 1987), or have no immediate effect on plant growth (Lee and Weber 1979; McColl and Firestone 1987). In this experiment, the effect of pH treatment on the final height of the two species was

only strongly indicated at the pH 1.0 level, especially for Artemisia seedlings grown on Santa Lucia soil. However, there were complex interactions between pH treatment, soil type, and species mixture that affected the growth of the seedlings. Although Pinus seedlings grew taller than Artemisia seedlings overall, particularly on Tangair soils, Artemisia seedlings had higher root production and greater root:shoot ratios. Artemisia also tended to grow taller in mixed culture than in pure culture. Artemisia therefore appears to be more sensitive to competition from the same species perhaps because of overlap in growth requirements (i.e. nutrients) than with a dissimilar species. Pinus muricata growth appears to be indifferent to its neighbors.

Species differences played a major role in determining the concentration of foliar nutrients. Overall, Artemisia seedlings had greater concentrations of both nitrogen and phosphorous in its foliage than Pinus seedlings. However, soil type appears to play an important role in determining total foliar nutrient accumulations. Santa Lucia soils tend to be more fertile than Tangair soils and total foliar accumulations of both nitrogen and phosphorous were greater on the Santa Lucia soil than the Tangair soil, in general, and for each species. The affect of pH treatment only weakly determined the concentration and accumulation of nitrogen and phosphorous in the foliage of the two species. The only clear pattern that emerged was the tendency for Artemisia seedlings grown on the Tangair soil to accumulate more nitrogen and phosphorous in mixed culture. It may be that when soil fertility is low competition for nutrient resources within this species is greater than when grown with Pinus muricata. There was no similar pattern for either nitrogen or phosphorous on the richer Santa Lucia soil or for Pinus seedlings on either soil.

Differences in yield between Artemisia californica and Pinus muricata tended to be greater between soil types rather than soil pH treatments, and yield was not

dependent on the sensitivity of the soil. Ashenden and Bell (1987) found similar results for winter barley grown on different soils with varying acid treatments. Zammit and Zedler (1988) showed that Artemisia yield was greater when grown on Santa Lucia soil than Tangair soils when treated with a single application of pH 2.5 or 5.6 HCl. In addition, they reported no survival of Artemisia seedlings at the pH 1.0 treatment. In this experiment, the yield of Artemisia, in general, was also higher on the Santa Lucia soil while yield of Pinus muricata was higher on the Tangair soil. The exception being the poor performance of Artemisia seedlings on the Santa Lucia soil treated with pH 1.0 HCl. It appears that Artemisia seedlings may be the more sensitive of the two species to differences in soil fertility and soil pH.

Despite the differences in height, biomass, and relative yield between the two species for the different soils types, acid treatments, and planting mixtures, there was no strong indication of a competitive advantage gained by either species. The poor performance or lack of survival of Artemisia seedlings on Santa Lucia soils treated with pH 1.0 HCl may be an indirect advantage to Pinus seedlings due to differences in plant sensitivity to lowered soil pH. This may indicate that as the number of shuttle launches increase as well as the number of deposition events to the soil, changes may occur in the recruitment and thus abundance of Artemisia californica on Santa Lucia soils where acid deposition is below pH 2.5. Hypothetically, Pinus seedlings would benefit in the long run because of reduced competition for resources. Resource competition between other species of pines growing with grass, shrubs, or other trees has been shown to significantly affect the growth, biomass, and yield of pine seedlings (Shainsky and Radosevich 1986; Cole and Newton 1987).

The susceptibility of coastal soils and vegetation, already subject to natural additions of HCl from the reaction between sea salt and air pollutants, may be enhanced by further burdens of HCl inputs such as those produced by repeated shuttle launches

(Endress et. al. 1978; Hinkle et. al. 1986). Hinkle et. al. (1986) reported that the pH of soil leachates from coastal soils declined as the number of shuttle launches increased and that the buffering capacity of the soil was lowered due to increased losses of base cations. The overall effect was a lowering of soil pH. Near-field and far-field plant community monitoring experiments around the shuttle launch site at Vandenberg Air Force Base are needed to document species composition changes and shifts in competitive regimes thru time in a natural setting.

EXPERIMENT 3: THE EFFECT OF DROUGHT ON GROWTH, BIOMASS PRODUCTION AND RELATIVE YIELD OF PINUS MURCATA and ARTEMISIA CALIFORNICA GROWING IN PURE AND MIXED CULTURE ON TWO SOILS.

This experiment was undertaken to determine the competitive interactions between Pinus muricata and Artemisia californica when grown under differing drought conditions and planting mixtures on their natural soils. The design layout from this experiment was used for the two preceding experiments. The hypothesis tested was in this experiment was that when exposed to drought Pinus muricata has a competitive advantage in growth, biomass, and relative yield over Artemisia californica on native soils.

METHODS

Planting

Santa Lucia and Tangair soils were collected from sites at Vandenberg AFB, passed through a 2mm. sieve to remove rocks, and placed into 250 cc. pots. In addition, Tangair soil was mixed 1:1 with quartz sand to make a third soil type that was theoretically more nutrient poor than just Tangair soil. Seeds of Pinus muricata and Artemisia californica were germinated in growth chambers prior to planting. Pairs

of seedlings were planted in pots of Santa Lucia and Tangair soil in two mixtures. Pure cultures consisted of either two Bishop pine or two Artemisia seedlings per pot. Mixed cultures contained one seedling of each species. The seedlings were allowed to grow in a covered greenhouse 1 month (March 1987) before beginning the drought treatments.

Drought Treatments

After the seedlings had grown for 1 month, the seedling mixtures on each soil type were randomly assigned one of two watering treatments, high or low, so that each species mixture and treatment was replicated 14 times (Table 17). The soil moisture was measured gravimetrically in unplanted pots of each soil type to monitor the soil water content which determined the watering interval. Seedlings in the high water treatment were not allowed to reach the wilting point: the soil was kept within the field capacity range (between 18-32% water content for the Santa Lucia soil; 10-26% for the Tangair soil). Seedlings in the low water treatment were watered only after the soil water content was at or very near the wilting point (between 8-10% water content for the Santa Lucia; 5-8% water content for the Tangair) or when the seedlings showed symptoms of wilting.. When the pots were watered the soils were always brought close to saturation and then allowed to drain to field capacity. The seedlings were grown for 3 months (April-June 1987) under these watering treatments.

Measurements and Analysis

The height of each seedling was measured at the beginning of the drought treatments and the growth of the seedlings monitored by calculating the change in height from monthly height measurements thereafter. Three months after the drought treatments were started a final height measurement was taken and the

seedlings were harvested. Total biomass for each seedling was fractioned into a shoot and root portion representing above and below ground production, respectively. Root-shoot ratios were calculated by dividing the total root biomass by the total shoot biomass for each species. Relative yields for the species were calculated by dividing the performance measure of a species in mixed culture by the same performance measure for that species in pure culture (Silvertown 1987).

This experiment was set up as a factorial experiment using a randomized-block design. A four-way analysis of variance was used to detect significant differences in growth and biomass. The 4 treatment factors of this model were species (A. californica; P. muricata), soil type (Santa Lucia; Tangair), planting mixture (Pure; Mixed), and drought treatment (High; Low).

RESULTS

Productivity

The relationships between species mixtures growing on different soils under varying competitive regimes and soil water levels in natural systems are likely to be interactive. The results of this experiment support this premise. The statistical results for height change, shoot biomass, root biomass, and total biomass production all had significant interaction terms (Tables 18-19). The results for root:shoot ratio involved only main effects (Table 19) which did not demonstrate clear relationships. Despite the lack of clear patterns statistically, some generalized conclusions can be made by examining the distribution of the means relative to the main factors; soil type, mixture, species, and water treatment (Table 20).

In general, Artemisia seedlings grew taller than Pinus seedlings on all soil types for all planting mixtures and water treatments (Table 20). The greatest height change for

Artemisia seedlings occurred on Santa Lucia soil in mixed culture. Despite this difference in overall growth, Pinus seedlings had a greater total biomass (dry weight) on the Tangair and Tangair/sand soils, especially under the high water treatment. This is reflected both in greater shoot and root biomass for Pinus seedlings grown on these soils and treatments. Artemisia seedlings, however, had more total biomass, and more shoot and root biomass, on the Santa Lucia soil, especially when grown in mixed culture. This suggests that on Santa Lucia soils Artemisia seedlings have an advantage over Pinus seedlings in both growth and biomass accumulation whether grown in pure or mixed culture regardless of the moisture status of the soil as defined in this experiment.

Results for root:shoot ratios indicate that Artemisia seedlings have a larger proportion of roots (ratios closer to or greater than 1) than Pinus seedlings for all mixtures and water treatments between species (Table 20). Root:shoot ratios appear not to have been affected by the drought treatments or the planting mixtures used. Ratios, in general, were larger on the Tangair and Tangair/sand soils reflecting, in part, the easier root penetration due to the lighter soil texture.

Relative yield

Results for height change on the different soil types indicate that Artemisia has a competitive advantage over Pinus on the Santa Lucia soil for both water treatments while Pinus has a slight competitive advantage on the Tangair/sand soil for both water treatments (Figure 7). Height change results for the Tangair soil indicate a lack of competitive interaction and a slight stimulation in growth for both species.

The results for total biomass show no distinct competitive advantage for either species over all treatments (Figure 8). Although Artemisia seedlings had higher relative biomass yields on the Santa Lucia soils they gained no significant advantage

over Pinus seedlings which were only slightly sensitive to the presence of the other species. Artemisia seedlings had lower relative biomass yields on the Tangair/sand and Tangair soil high water treatments, but the Pinus seedlings gained no significant advantage. Both species responded positively on the Tangair/sand soil under the low water treatment.

DISCUSSION

Differences in the performance of Pinus and Artemisia found between soil types may be an indication of differences in the water relations of the soils and differences in soil fertility. In general, the Santa Lucia soils are the more fertile, have a greater water holding capacity, and tend to dry slower than the sandier Tangair and Tangair/sand soils which have better drainage and aeration but dry much more quickly (U.S.D.A. 1972). The greater productivity and relative yields for Artemisia seedlings on the Santa Lucia soil over the Tangair soils suggests that it is more sensitive to either changes in fertility, or soil water status, or both, than the Pinus seedlings which grew consistent across all soils and drought treatments.

The difference in growth-form of the two species (shrub vs. tree) may also account for the between species differences. Shrub seedlings tend to grow much faster during the initial phases of establishment when compared to early growth in pines. Water stress may act to enhance this difference. Shainsky and Radosevich (1986) found that soil moisture was depleted more in mixed plantings of Pinus ponderosa and Arctostaphylos patula than in pure cultures of Pinus suggesting competition for moisture. This lead to reduced Pinus productivity during the early stages of development when grown with Arctostaphylos. Competition for moisture may be a factor affecting growth between Artemisia and Pinus in this experiment since drought treatment was significant, interactively, only for this performance measure.

Growth of pine seedlings have been shown to be sensitive to increasing drought in other studies (e.g. Kaufmann 1968).

The general pattern that emerged from this experiment was the advantage Artemisia seedlings had on Santa Lucia soil particularly when grown with Pinus seedlings. The overall response of pine seedlings to the presence of Artemisia was essentially neutral with respect to soil type and soil water status. Although the drought treatments played only a minor role in determining differences between species in this experiment, the soil water status of Santa Lucia and Tangair soils in nature, along with other soil factors, undoubtedly play an important role in the distribution of species.

REFERENCES

- Aber, J.D. , G.R. Hendrey, D.B. Botkin, A.J. Francis, and J.M. Mellillo 1982. Potential effects of acid precipitation on soil nitrogen and productivity of forest ecosystems. *Water, Air, Soil Pollution* 18:405-412.
- Abrahamsen, G. , R. Horntvedt, and B. Tverte 1977. Impacts of acid precipitation on coniferous forest ecosystems. *Water, Air, Soil Pollution* 8:57-73.
- Anderson, B.J. and V.W. Keller 1983. Space Shuttle Exhaust Cloud Properties. NASA Technical Paper 2258, Marshall Space Flight Center, Alabama.
- Armentano, T.V. and E.S. Menges 1987. Air-pollution-induced foliar injury to natural populations of Jack and White pine in a chronically polluted environment. *Water, Air, and Soil Pollution* 33:395-409.
- Ashenden, T.W. and S. Bell 1987. Yield reductions in winter barley grown on a range of soils and exposed to simulated acid rain. *Plant and Soil* 98:433-437.
- Bache, B.W. 1980. The sensitivity of soils to acidification. pp. 569-572, in T.C. Hutchinson and M. Havas (eds.) *Effects of Acid Precipitation on Terrestrial Ecosystems*. Plenum Press, New York.

- Baker J. and D. Hocking 1977. Acidity of open and intercepted precipitation in forests and effects on forest soils in Alberta, Canada. *Water, Air, Soil Pollution* 7:449-460.
- Cole, C.V. and J.W.B. Stewart 1983. Impact of acid deposition on Phosphorous cycling. *Environmental and Experimental Botany* 23(3):235-241.
- Cole, E.C. and M. Newton 1987. Fifth year response of Douglas-fir to crowding and non-coniferous competition. *Canadian J. Forestry Research* 17:181-186.
- Connolly, J. 1986. On difficulties with replacement series methodology in mixture experiments. *J. of Applied Ecology* 23:125-137.
- Connolly, J. 1987. On the use of response models in mixture experiments. *Oecologia* 72:95-103.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *American Midland Naturalist* 122(5):661-696.
- Coulombe, H.N. and C.R. Mahrdt (eds). 1976. *Ecological Assessment of Vandenburg Air Force Base, California: Vol. II Biological Inventory 1974/5*. Air Force Civil Engineering Technical Report 76-15, Los Angeles Air Force Station, California.
- Davidson, I.A. and M.J. Robson 1986. Effect of temperature and nitrogen supply on the growth of perennial ryegrass and white clover: II. A comparison of monocultures and mixed swards. *Annals of Botany* 57(5):709-719.

- Duffield, J.W. 1951. Interrelationships of the California closed-cone pines with special reference to *Pinus muricata* D. Don. Phd. Thesis, University of California, Berkeley. 77pp.
- Endress, A.G. , R.J. Oshima, and O.C. Taylor 1979. Age-dependent growth and injury responses of Pinto Bean leaves to gaseous hydrogen chloride. *J. of Environmental Quality* 8(2):260-264.
- Endress, A.G. , T.J. Swiecki, and O.C. Taylor 1978. Foliar and microscopic observations of bean leaves exposed to hydrogen chloride gas. *Environmental and Experimental Botany* 18:139-149.
- Evans, L.S. , K.F. Lewin, E.M. Owen, and K.A. Santucci 1986. Comparison of yields of several cultivars of field-grown soybeans exposed to simulated acidic rainfalls. *New Phytologist* 102:409-417.
- Evans, L.S. , N.F. Gmur, and F. DaCosta 1977. Leaf surface and histological perturbations of leaves of Phaseolus vulgaris and Helianthus annuus after exposure to simulated acid rain. *Amer. J. Bot.* 64:903-913.
- Evans, L.S. and T.M. Curry 1979. Differential response of plant foliage to simulated acid rain. *American J. Botany* 66:953-962.
- Firbank, L.G. and A.R. Watkinson 1987. On the analysis of competition at the level of the individual plant. *Oecologia* 71:308-317.

- Granett, A.L. 1983. Effect of acidic deposition on economic plants in the Vandenburg area. Proceedings of NASA/USAF Space Shuttle Environmental Conference, Kennedy Space Center, Florida. Dec. 14-16, 1982.
- Granett, A.L. and O.C. Taylor 1981. Diurnal and seasonal changes in sensitivity of plants to short exposures of Hydrogen chloride gas. *Environment and Agriculture* 6:33-42.
- Haines, B. , M. Stefani, and F. Hendrix 1980. Acid rain: Threshold of leaf damage in eight plant species from a Southern Appalachian forest succession. *Water, Air, and Soil Pollution* 14:403-407.
- Harper, J.L. 1977. *Population Biology of Plants*. Academic Press, London.
- Heywood, J.S. and D.A. Levin 1986. Interactions between seed source, planting arrangement, and soil treatment in determining plant size and root allocation in *Phlox drummondii*. *Oecologia* 68(2):285-290.
- Hinkle, C.R. , T.L. Hughes, and P.A. Schmalzer 1986. Evaluations of the effects of acidification on coastal soils. Poster presented at the Ecological Society of America Annual meeting, August 10-16, 1986, Syracuse University, New York.
- Jacbson, J.S. , J. Osmeloski, K. Yamada, and L. Heller 1987. The influence of simulated acid rain on vegetative and reproductive tissues of cucumber (*Cucumis sativus* L.). *New Phytologist* 105:139-147.

- Johnson, D.W. , J. Turner, and J. M. Kelly 1982. The effects of acid rain on forest nutrient status. *Water Resources Research* 18:449-461.
- Kaufmann, M.R. 1968. Water relations of pine seedlings in relation to root and shoot growth. *Plant Physiology* 43:281-288.
- Kelly, J.M. and R.C. Strickland 1987. Soil nutrient leaching in response to simulated acid rain treatment. *Water, Air, and Soil Pollution* 34:167-181.
- Lee, J.J. , G.E. Neely, S.C. Perrigan, and L.C. Grothaus 1981. Effect of simulated acid rain on yield, growth, and foliar injury of several crops. *Environmental and Experimental Botany* 21(2):171-185.
- Lee, J.J. and D.E. Weber 1979. The effect of simulated acid rain on seedling emergence and growth of eleven woody species. *Forest Science* 25(3):393-398.
- Lerman, S. , O.C. Taylor, and E.F. Darley 1976. Phytotoxicity of hydrogen chloride gas with a short term exposure. *Atmospheric Env.* 10:873-878.
- Lind, C.T. and S.A. London 1971. Exposure of Marigold (*Tagetes*) to gaseous hydrogen chloride. Aerospace Medical Research Laboratory Technical Report 71-90, Wright-Patterson Air Force Base, Ohio.
- Malanson, G.P. and W.E. Westman 1985. Postfire succession in Californian coastal sage scrub: The role of continual basal sprouting. *American Midland Naturalist* 113(2):309-318.

- Maurice, C.G. and R.E. Crang 1986. Increase in *Pinus strobus* needle transectional areas in response to acidic misting. *Archives of Environmental Contamination and Toxicology* 15:77-82.
- McColl, J.G. , and M.K. Firestone 1987. Cumulative effects of simulated acid rain on soil chemical and microbial characteristics and conifer seedling growth. *Soil Science Society of America Journal* 51(3):794-800.
- McColl, J.G. and R. Johnson 1983. Effects of simulated acid rain on germination and early growth of Douglas-fir and Ponderosa pine. *Plant and Soil* 74:125-129.
- McFee, W.W. 1983. Sensitivity ratings of soils to acid deposition: A review. *Environmental and Experimental Botany* 23(3):203-210.
- Mead, R. 1979. Competition experiments. *Biometrics* 35(1):41-54.
- Olson, R.L., Jr. , W.E. Winner, and L.D. Moore 1987. Effects of "pristine" and "industrial" simulated acid precipitation on greenhouse-grown radishes. *Environmental and Experimental Botany* 27(2):239-244.
- Pell, E.J., C.J. Arny, and N.S. Pearson 1987. Impact of simulated acidic precipitation on quantity and quality of a field grown potato crop. *Environmental and Experimental Botany* 27(1):7-14.
- Percy, K. 1986. The effects of simulated acid rain on germinative capacity, growth, and morphology of forest tree seedlings. *New Phytologist* 104:473-484.

- Percy, K.E. and E.A. Baker 1987. Effects of simulated acid rain on production, morphology, and composition of epicuticular wax and on cuticular membrane development. *New Phytologist* 107:577-589.
- Peterson, L. 1980. Sensitivity of different soils to acid precipitation. pp. 573-577, in T.C. Hutchinson and M. Havas (eds.) *Effects of Acid Precipitation on Terrestrial Ecosystems*. Plenum Press, New York.
- Raynal, D.J. , J.R. Roman, and W.M. Eichenlaub 1982. Response of tree seedlings to acid precipitation- I. Effects of substrate acidity on seed germination. *Env. Exper. Bot* 22:377-383.
- Reich, P.B. , A.W. Schoettle, H.F. Stroo, J. Troiano, and R.G. Amundson 1987. Effects of ozone and acid rain on White pine (*Pinus strobus*) seedlings grown in five soils. I. Net photosynthesis and growth. *Canadian J. Botany* 65:977-987.
- Reuss, J.O. 1980. Simulation of soil nutrient losses resulting from rainfall acidity. *Ecological Modelling* 11:15-38.
- Reuss, J.O. and D.W. Johnson 1986. Acid deposition and the acidification of soils and waters. *Ecological Studies* Vol. 59. Springer-Verlag, New York.
- Scherbatskoy, T. , R.M. Klein, and G.J. Badger 1987. Germination response of forest tree seeds to acidity and metal ions. *Env. Exper. Bot.* 27:157-164.
- Scherbatskoy, T. and R.M. Klein 1983. Response of spruce and birch foliage to leaching by acidic mists. *J. Env. Quality* 12:189-194.

- Schier, G.A. 1986. Seedling growth and nutrient relationships in a New Jersey Pine Barrens soil treated with "acid rain". *Canadian J. of Forestry Research* 16:136-142.
- Schmalzer, P.A., C.R. Hinkle, and D. Breininger 1985. Effects of space shuttle launches STS-1 through STS-9 on terrestrial vegetation of John F. Kennedy Space Center, Florida. NASA Technical Memorandum 83103, J.F.K. Space Center, Florida.
- Schmalzer, P.A., C.R. Hinkle, and T.W. Dreschel 1986. Far field deposition from space shuttle launches at John F. Kennedy Space Center, Florida. NASA Technical Memorandum 83104, J.F.K. Space Center, Florida.
- Schoener, T.W. 1983. Field experiments of interspecific competition. *American Midland Naturalist* 122(2):240-285.
- Shainsky, L.J. and S.R. Radosevich 1986. Growth and water relations of *Pinus ponderosa* seedlings in competitive regimes with *Arctostaphylos patula* seedlings. *J. of Applied Ecology* 23:957-966.
- Sih, A. , P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier 1985. Predation, competition, and prey communities: A review of field experiments. *Annual Review of Ecology and Systematics* 16:269-311.
- Silvertown, J. 1987. *Introduction to Plant Population Ecology*. John Wiley and Sons, Inc., New York.

- Smith, C.F. 1976. A Flora of Santa Barbara Region, California. Santa Barbara Museum of Natural History, Santa Barbara, California.
- Snaydon, R.W. 1979. A new technique for studying plant interactions. *J. of Applied Ecology* 16(1):281-286.
- State University of New York 1982. Proceedings of the Acid Precipitation Research Needs Conference; Huntington Wildlife Forest, Newcomb, New York. State University of New York, College of Environmental Science and Forestry, Syracuse, New York.
- State University of New York 1984. Effects of acidic deposition on forest ecosystems in the Northeastern United States: An evaluation of current evidence. State University of New York, College of Environmental Science and Forestry, Syracuse, New York.
- Stroo, H.F. and M. Alexander 1986. Available nitrogen and nitrogen cycling in forest soils exposed to simulated acid rain. *Soil Science Society of America Journal* 50:110-114.
- Tamm, C.O. and E.B. Cowling 1977. Acidic precipitation and forest vegetation. *Water, Air, Soil Pollution* 7:503-511.
- Technicon 1987a. Nitrate and Nitrite in water. Industrial Method 158-71 W/A, Technicon AutoAnalyzer II.

- Technicon 1987b. Ammonia in water and seawater. Industrial Method 154-71 W, Technicon AutoAnalyzer II.
- Technicon 1987c. Ortho-phosphate in water. Industrial Method 155-71W, Technicon AutoAnalyzer II.
- Technicon 1987d. Individual/Simultaneous determination of Nitrogen and/or Phosphorous in BD acid digests. Industrial Method 329-74 W/B, Technicon AutoAnalyzer II.
- Temple, P.J. , R.W. Lennox , A. Bytnerowicz, and O.C. Taylor 1987. Interactive effects of simulated acidic fog and ozone on field-grown alfalfa. *Environmental and Experimental Botany* 27(4):409-417.
- U.S.D.A. 1972. Soil Survey of Northern Santa Barbara Area, California. U.S. Department of Agriculture Soil Conservation Service, Washington D.C.
- Wiklander, L. 1980. The sensitivity of soils to acid precipitation. pp. 553-567, in T.C. Hutchinson and M. Havas (eds.) *Effects of Acid Precipitation on Terrestrial Ecosystems*. Plenum Press, New York.
- Wood, T. and F.H. Bormann 1977. Short-term effects of a simulated acid rain upon the growth and nutrient relations of *Pinus strobus* L. *Water, Air, and Soil Pollution* 7:479-488.

Zammit, C.A. and P.H. Zedler 1988. Germination response to extreme acidity:
Impact of simulated acid deposition from a single shuttle launch.
Environmental and Experimental Botany 28(1):73-81.

Table 1. Experimental design for the foliar acid treatment experiment in which three month old Pinus muricata (P) and Artemisia californica (A) seedlings were treated with a single application of either pH 1.0 HCl acid or deionized water. Seedlings were planted in two mixtures (PP, AA = pure cultures; PA = mixed culture). Values indicate the number of pots (replicates) in each treatment.

Planting Mixture: AA PP PA

Treatment:

Acid 10 10 10

Water 10 10 10

TABLE 2. Results of the three-way ANOVA for growth of *Artemisia* and *Pinus* seedlings treated with a single foliar application of pH 1.0 HCl. Log transformed means used for the analysis. (* $P \leq .05$; ** $P \leq .01$; *** $P \leq .0001$)

		F-ratios				
	df.	Growth	Shoot biomass	Root biomass	Total biomass	Root:shoot ratio
Source:						
species	1	***18.92	***48.05	***22.00	***39.18	0.816
mix	1	.0055	0.59	2.73	1.46	*4.64
treatment	1	***25.59	*6.83	1.63	*4.71	0.816
sp x mix	1	.634	.0009	0.272	0.041	0.062
sp x treat	1	**12.87	**14.06	**9.40	**13.05	0.194
mix x treat	1	**12.54	0.957	0.468	0.857	0.00001
sp x mix x treat	1	**15.69	*6.64	2.95	*5.12	0.007
error	30					

Table 3. Means per plant (n=10) for growth and biomass of *Pinus* and *Artemisia* seedlings treated with a single application of pH 1.0 HCl or distilled water. Values in parentheses are standard deviations.

planting mixture: treatment	Pure		Mixed	
	Acid	Water	Acid	Water

HEIGHT CHANGE (cm)				
<i>Pinus muricata</i>	.067 (.13)	.267 (.10)	.200 (.10)	.325 (.23)
<i>Artemisia californica</i>	.767 (.72)	.967 (.88)	-.167 (.37)	2.025 (.45)
SHOOT BIOMASS (g.)				
<i>Pinus muricata</i>	.173 (.01)	.167 (.02)	.141 (.04)	.180 (.02)
<i>Artemisia californica</i>	.096 (.006)	.073 (.01)	.131 (.03)	.056 (.03)
ROOT BIOMASS (g.)				
<i>Pinus muricata</i>	.099 (.01)	.110 (.02)	.073 (.04)	.094 (.02)
<i>Artemisia californica</i>	.060 (.02)	.044 (.01)	.072 (.03)	.032 (.02)
TOTAL BIOMASS (g.)				
<i>Pinus muricata</i>	.272 (.02)	.277 (.04)	.214 (.08)	.274 (.04)
<i>Artemisia californica</i>	.156 (.02)	.117 (.02)	.204 (.06)	.089 (.06)
ROOT SHOOT RATIO				
<i>Pinus muricata</i>	.575 (.07)	.660 (.08)	.483 (.18)	.519 (.06)
<i>Artemisia californica</i>	.706 (.40)	.743 (.44)	.537 (.12)	.570 (.14)

Table 5. Results of two-way ANOVA for the pH of soil from the pots of the 1.0, 2.5, 5.6 acid treatments for the Santa Lucia and Tangair soils. (***) $P < .0001$)

Source:	d.f.	F-ratio
soil	1	889.71***
pH	2	101.41***
soil x pH	2	12.24***
error	283	

Table 6. Mean pH of soil from the pots of the various acid treatments for the two soil types. Standard deviations are in parentheses.

pH Treatment	1.0	2.5	5.6
Santa Lucia	3.90 (.22)	4.23 (.27)	4.46 (.29)
Tangair	4.80 (.23)	5.35 (.23)	5.22 (.31)

Table 7. Results of the repeated measures ANOVA for the pH of the leachate from Santa Lucia and Tangair soils treated with pH 1.0, 2.5, or 5.6 HCl and leached with water 5 times. (*** $P < .0001$)

Source:	df.	F-ratio
<hr/>		
pH treatment	2	133.26***
soil	1	525.99***
pH treat. x soil	2	13.85***
subjects within groups	24	
Repeated measure	4	19.97***
(Number of leachings)		
pH treat. x Rep. meas.	8	7.18
soil x Rep. meas.	4	33.56***
pH treat. x soil x Rep. meas.	8	1.36
Rep. meas. x subjects -		
within groups	96	
<hr/>		

Table 9. Results of the two-way ANOVA's for total release of Nitrate (NO_3), ammonia (NH_4), and phosphate (PO_4) from Santa Lucia and Tangair soils treated with acid and leached with water 5 times. Analysis was performed on log transformed means.

(*** $P < .001$)

Source:	df:	F-ratio
---------	-----	---------

NO_3

soil	1	23.08***
pH treat	2	0.474
soil x pH treat	2	.253
error	24	

NH_4

soil	1	17.96***
pH treat	2	2.64
soil x Ph treat	2	0.305
error	24	

PO_4

soil	1	.0002
pH treat	2	0.452
soil x pH treat	2	0.341
error	24	

Table 10. Mean total nutrient loss (ppm) for nitrate (NO₃), ammonia (NH₄), and phosphate (PO₄) by soil type and pH treatment. Standard deviations are in parentheses.

Soil Type: pH Treatment:	Santa Lucia		Tangair	
	1.0	2.5	1.0	2.5
Nutrient:				
NO ₃	674.3 (452.3)	535.7 (369.1)	170.8 (82.6)	132.4 (94.6)
NH ₄	12.1 (9.9)	7.0 (5.4)	53.9 (33.6)	15.9 (7.3)
PO ₄	0.86 (0.49)	0.97 (0.68)	1.32 (0.90)	0.63 (0.30)
				0.89 (0.67)

Table 11. Four-way ANOVA results for growth of Artemisia californica and Pinus muricata seedlings grown in pure and mixed cultures on Tangair and Santa Lucia soils treated with acid. The analysis was performed on log transformed data. (* $P \leq .05$; ** $P \leq .01$; *** $P \leq .0001$)

				F-ratios		
	df.	Growth	biomass	biomass	biomass	ratio
species	1	***13.04	***46.65	**10.65	***28.63	**11.86
soil	1	2.59	0.16	1.48	0.21	*6.02
mix	1	1.35	0.55	0.27	0.56	0.09
pH treatment	2	0.70	*4.43	*4.62	**5.04	2.52
sp. x soil	1	0.04	0.04	0.63	0.17	2.44
sp. x mix	1	0.35	1.36	0.23	0.99	0.99
sp. x pH treat.	2	2.03	**6.95	*4.27	**6.42	0.09
soil x mix	1	0.66	0.47	1.30	0.88	.089
soil x pH treat.	2	*4.55	**7.57	*4.14	**6.39	*3.43
pH treat. x mix	2	2.28	*4.57	*3.84	**5.37	0.05
sp x soil x pH treat.	2	**5.05	1.40	**7.54	0.99	0.40
sp. x soil x mix	1	0.50	***9.86	0.29	***9.58	0.50
sp. x pH treat. x mix	2	2.47	**5.74	**5.55	**6.58	0.30
soil x pH x mix	2	1.12	0.94	1.50	0.87	*2.90
error	187					

Table 12. Means for growth and biomass for *Artemisia californica* and *Pinus muricata* seedlings grown on acid treated Santa Lucia and Tangair soils in pure and mixed cultures. Values in parentheses are standard deviations. (* denotes small sample)

Soil type: pH Treatment: Planting mixture:	SANTA LUCIA				TANGAIR			
	1.0		5.6		1.0		2.5	
	pure	mix	pure	mix	pure	mix	pure	mix
Height change (cm)								
<u>Pinus</u>	4.66 (.72)	5.31 (.89)	4.56 (.63)	4.62 (.73)	4.55 (.71)	4.66 (.99)	4.3 (.68)	4.2 (.81)
<u>Artemisia</u>	----- *	2.0 *	4.28 (.97)	6.48 (3.7)	3.76 (.29)	6.34 (4.3)	2.7 *	2.3 (1.9)
Shoot Biomass (gm.)								
<u>Pinus</u>	.137 (.02)	.158 (.05)	.124 (.03)	.118 (.04)	.142 (.02)	.118 (.06)	.126 (.02)	.125 (.03)
<u>Artemisia</u>	----- *	.014 *	.117 (.04)	.153 (.12)	.079 (.01)	.193 (.13)	.032 *	.028 (.02)
Root Biomass (gm.)								
<u>Pinus</u>	.078 (.04)	.086 (.03)	.047 (.02)	.06 (.02)	.077 (.02)	.075 (.04)	.062 (.01)	.073 (.03)
<u>Artemisia</u>	----- *	.007 *	.078 (.04)	.096 (.06)	.069 (.03)	.178 (.15)	.031 *	.027 (.02)
Total Biomass (gm.)								
<u>Pinus</u>	.214 (.06)	.245 (.09)	.172 (.05)	.178 (.06)	.219 (.04)	.193 (.09)	.188 (.02)	.199 (.06)
<u>Artemisia</u>	----- *	.021 *	.195 (.05)	.249 (.17)	.148 (.04)	.371 (.24)	.064 *	.056 (.05)
Root:Shoot Ratio								
<u>Pinus</u>	.554 (.24)	.543 (.07)	.37 (.09)	.52 (.09)	.57 (.19)	.75 (.56)	.48 (.11)	.57 (.16)
<u>Artemisia</u>	----- *	.48 *	.61 (.30)	.64 (.22)	1.11 (.69)	.96 (.90)	1.27 *	1.1 (.72)

TABLE 13. Results from 4-way ANOVA for concentration of nitrogen and phosphorous (mg/gm) in foliage of Pinus muricata and Artemisia californica seedlings grown on acid treated Santa Lucia and Tangair soils for pure and mixed cultures. Log transformed data used for the analysis. (* $P \leq .05$; ** $P \leq .01$; *** $P \leq .0001$)

Source:	df.	-----F-ratios-----	
		Nitrogen	Phosphorous
species	1	***52.78	***33.19
soil	1	2.80	3.02
pH treatment	2	1.82	1.01
mixture	1	*5.38	0.689
sp. x soil	1	2.86	0.299
sp. x pH treat.	2	2.15	0.622
sp. x mix	1	0.238	2.65
soil x pH treat.	2	1.42	2.67
soil x mix	1	0.235	0.757
pH treat. x mix	2	2.67	1.29
sp. x soil x pH treat.	2	2.68	2.37
sp. x soil x mix	1	0.158	3.23
sp. x pH treat. x mix	2	**5.36	0.643
soil x pH treat. x mix	2	*3.13	0.895
error	198		

TABLE 14. Mean concentration (mg/gm) of nitrogen and phosphorous in foliage of *Pinus muricata* and *Artemisia californica* seedlings grown on acid treated Santa Lucia and Tangair soils for pure and mixed cultures. Values in parentheses are standard deviations.

Soil type: pH treatment: Mixture:	SANTA LUCIA				TANGAIR			
	1.0		5.6		1.0		5.6	
	pure	mix	pure	mix	pure	mix	pure	mix
Nitrogen (mg/gm)								
<i>Pinus muricata</i>	16.49 (2.34)	17.65 (3.43)	18.23 (6.01)	18.41 (5.37)	14.53 (1.83)	18.10 (5.66)	14.71 (1.30)	14.55 (2.88)
<i>Artemisia californica</i>	— ***	29.40 ***	25.70 (7.72)	26.05 (8.99)	24.62 (5.09)	22.57 (4.43)	26.71 (6.51)	30.93 (4.87)
							30.04 (5.90)	21.65 (3.32)
Phosphorous (mg/gm)								
<i>Pinus muricata</i>	0.70 (.15)	0.67 (.26)	1.01 (.72)	1.05 (1.0)	0.53 (.13)	1.11 (1.2)	0.68 (.12)	0.62 (.28)
<i>Artemisia californica</i>	— ***	1.39 ***	1.26 (.36)	1.15 (.71)	1.07 (.13)	0.90 (.40)	1.28 ***	0.94 (.19)
							1.11 (.40)	1.30 (.38)
							1.15 (.14)	1.30 (.02)

TABLE 15. Results of the 4-way ANOVA for total accumulation of nitrogen and phosphorous (mg/seedling) in foliage of Artemisia californica and Pinus muricata seedlings grown in pure and mixed cultures on acid treated Santa Luica and Tangair soils. Log transformed values used in the analysis.

(* $P \leq .05$; ** $P \leq .01$)

Source:	-----F-ratios-----	
	Nitrogen	Phosphorous
species	0.18	1.97
soil	*5.63	**0.009
pH treatment	0.20	0.08
mixture	*6.55	1.73
sp. x soil	0.05	0.16
sp. x pH treat.	*3.28	1.40
sp. x mixture	**11.78	*4.88
soil x pH treat.	0.80	0.29
soil x mixture	0.31	2.32
pH treat. x mix.	0.04	1.71
sp. x soil x pH treat.	0.76	0.68
sp. x soil x mix.	0.10	*6.56
sp. x pH treat. x mix.	0.01	2.16
soil x pH treat. x mix.	0.18	0.32

Table 16. Mean total accumulation of nitrogen and phosphorous in the foliage of *Artemisia californica* and *Pinus muricata* seedlings grown in pure and mixed culture on acid treated Santa Lucia and Tangair soils. Values in parentheses are standard deviations.

Soil type: pH treatment: Mixture:	Santa Lucia				Tangair			
	1.0		2.5		5.6		1.0	
	pure	mix	pure	mix	pure	mix	pure	mix
Nitrogen								
(mg/seedling)								
<u><i>Pinus muricata</i></u>	1.81 (.54)	2.15 (.69)	1.71 (.59)	1.37 (.75)	1.71 (.41)	2.36 (1.7)	1.55 (.27)	1.32 (.55)
							1.35 (.35)	1.01 (.70)
								5.6 pure mix
<u><i>Artemisia californica</i></u>	— ***	3.91 ***	1.99 (.27)	2.65 (1.3)	2.65 (1.7)	1.87 (.98)	0.22 ***	2.63 (1.3)
							1.38 (.78)	3.11 (1.2)
								1.04 (.55)
								1.77 (.67)
Phosphorous								
(mg/seedling)								
<u><i>Pinus muricata</i></u>	0.077 (.023)	0.078 (.021)	0.092 (.069)	0.067 (.034)	0.063 (.020)	0.147 (.177)	0.073 (.018)	0.055 (.027)
							0.057 (.015)	0.039 (.028)
								0.052 (.028)
								0.065 (.024)
<u><i>Artemisia californica</i></u>	— ***	0.185 ***	0.099 (.021)	0.123 (.105)	0.115 (.069)	0.072 (.050)	0.020 ***	0.104 (.021)
							0.054 (.020)	0.131 (.063)
								0.042 (.022)
								0.105 (.023)

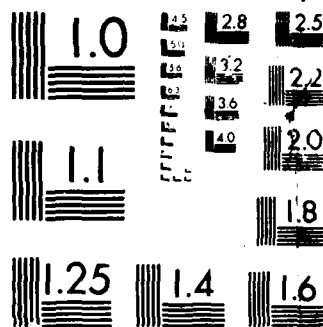
Table 17. Experimental design for the drought experiment involving Pinus muricata (P) and Artemisia californica (A) growing on two natural soils (Santa Lucia; Tangair) and one soil mixture (Tangair + Sand) in two planting mixtures (PP, AA = pure cultures; PA = mixed culture). Values indicate the number of pots (replicates) in each treatment.

[illegible]

TABLE 18. Results of the 4-way ANOVA for growth of Pinus muricata and Artemisia californica seedlings growing on Santa Lucia and Tangair soils in pure and mixed cultures under high and low water stress. Log transformed data used for the analysis (*- $P \leq .05$; **- $P \leq .01$; ***- $P \leq .0001$)

	df.	F-ratio

Growth		
Source:		
species	1	***237.94
soil	2	***32.47
mix	1	0.035
treatment	1	0.034
sp. x soil	2	***26.80
sp. x mix	1	*4.77
sp. x treat.	1	*4.62
soil x mix	2	0.92
soil x treat.	2	0.20
mix x treat.	1	1.99
sp. x soil x mix	2	**6.50
sp. x soil x treat.	2	*3.39
sp. x mix x treat.	1	0.31
soil x mix x treat.	2	0.70
sp. x soil x mix x treat.	2	0.76
error	188	



MICROCOPY RESOLUTION TEST CHART
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TABLE 19. Results of the 4-way ANOVA for shoot, root, and total biomass and root:shoot ratios of Pinus muricata and Artemisia californica seedlings growing on Santa Lucia and Tangair soils in pure and mixed cultures under high and low water stress. Log transformed data used for the analysis.

(*- $P \leq .05$; **- $P \leq .01$; ***- $P \leq .0001$)

	df.	F-ratios			
		Shoot biomass	Root biomass	Total biomass	Root:shoot ratio
Source:					
species	1	***48.53	.004	**11.73	***47.69
soil	2	***63.59	***9.52	***35.08	***10.74
mix	1	1.32	1.63	1.73	0.29
treatment	1	1.41	2.46	2.07	1.85
sp. x soil	2	***76.24	***26.19	***58.35	0.55
sp. x mix	1	2.12	0.09	1.31	2.05
sp. x treat.	1	0.005	0.78	0.16	1.58
soil x mix	2	1.21	1.75	1.89	1.84
soil x treat.	2	1.32	0.55	0.67	1.47
mix x treat.	1	0.65	0.11	0.27	0.03
sp. x soil x mix	2	**4.74	0.72	2.77	0.72
sp. x soil x treat.	2	0.98	0.22	0.23	1.18
sp. x mix x treat.	1	0.17	0.003	0.16	0.06
soil x mix x treat.	2	1.86	1.51	2.11	0.18
sp. x soil x mix x treat.	2	0.89	1.77	1.72	0.87
error	211				

TABLE 20. Means for growth, shoot biomass, root biomass, total biomass, and root:shoot ratios for *Artemisia* and *Pinus* seedlings grown on Santa Lucia and Tangair soils in pure and mixed cultures under high and low water treatments. Values in parentheses are standard deviations.

Planting mixture: Soil: Water Treatment	Santa Lucia			Pure Tangair		Tangair/Sand		Santa Lucia/Tangair		Mixed		Tangair/Sand		Low	High	Low	High
	High	Low	(.57)	High	Low	High	Low	High	Low	High	Low	High	Low				
HEIGHT CHANGE (cm)																	
<i>Pinus muricata</i>	3.0	2.95	(.67)	2.25	2.15	2.13	2.27	1.88	2.16	2.47	2.33	2.01	2.37	2.01	(.72)	2.37	(1.3)
<i>Artemisia californica</i>	7.4	6.91	(1.17)	4.14	3.92	4.21	2.89	10.96	8.88	4.26	4.94	3.82	3.25	3.82	(1.6)	3.25	(1.1)
SHOOT BIOMASS (g.)																	
<i>Pinus muricata</i>	.17	.161	(.05)	.156	.148	.17	.152	.142	.138	.156	.147	.17	.175	.17	(.02)	.175	(.04)
<i>Artemisia californica</i>	.205	.20	(.05)	.081	.077	.067	.05	.414	.308	.067	.094	.057	.062	.057	(.02)	.062	(.02)
ROOT BIOMASS (g.)																	
<i>Pinus muricata</i>	.098	.08	(.04)	.114	.112	.152	.138	.111	.087	.111	.098	.158	.147	.158	(.05)	.147	(.02)
<i>Artemisia californica</i>	.167	.188	(.02)	.093	.063	.067	.078	.415	.227	.072	.093	.08	.10	.08	(.05)	.10	(.05)
TOTAL BIOMASS (g.)																	
<i>Pinus muricata</i>	.267	.241	(.09)	.27	.26	.322	.289	.252	.225	.267	.245	.327	.322	.327	(.06)	.322	(.06)
<i>Artemisia californica</i>	.373	.388	(.07)	.174	.14	.154	.127	.829	.535	.138	.187	.137	.162	.137	(.07)	.162	(.08)
ROOT:SHOOT RATIO																	
<i>Pinus muricata</i>	.617	.469	(.30)	.717	.738	.865	.868	.779	.643	.733	.648	.932	.855	.932	(.29)	.855	(.08)
<i>Artemisia californica</i>	1.0	.981	(.30)	1.23	1.0	1.19	1.48	1.04	.832	.983	.923	1.37	1.58	1.37	(.51)	1.58	(.32)

FIGURE LEGENDS

Figure 1. Graphical presentation of relative yields used to determine direction and magnitude of interactions between two species. If the value lies in the upper left hand quadrant (-A, +P) or the lower right hand quadrant (+A, -P) this suggests that one species has a competitive advantage over the other. Values lying in the lower left hand quadrant (-A, -P) or the upper right hand quadrant (+A, +P) indicate no species advantage, both react either negatively (antagonism) or positively (synergism) to the presence of the other species. The intersection of the relative yield = 1 lines indicates a neutral interaction.

Figure 2. Relative yields expressed as final height of Artemisia and Pinus seedlings 1 month after a foliar application of pH 1.0 HCl. Water treatment acted as the control.

Figure 3. Relative yields expressed as total biomass of Artemisia and Pinus seedlings 1 month after a foliar application of pH 1.0 HCl. Water treatment acted as the control.

Figure 4 a-c. a) The cumulative loss of nitrate (NO_3) from Santa Lucia and Tangair soils repeatedly treated with HCl solutions of varying pH and leached with water. b) The cumulative loss of ammonia (NH_4) from Santa Lucia and Tangair soils repeatedly treated with HCl solutions of varying pH and leached with water. c) The cumulative loss of phosphate (PO_4) from Santa Lucia and Tangair soils repeatedly treated with HCl solutions of varying pH and leached with water. (SL= Santa Lucia soil; T= Tangair soil)

Figure 5. Relative yields expressed as final height of Artemisia californica and Pinus muricata seedlings grown on Santa Lucia and Tangair soils pre-treated with pH 1.0, 2.5, or 5.6 HCl.

Figure 6. Relative yields expressed as total biomass of Artemisia californica and Pinus muricata seedlings grown on Santa Lucia and Tangair soils pre-treated with pH 1.0, 2.5, or 5.6 HCl.

Figure 7. Relative yields expressed as height change of Artemisia californica and Pinus muricata seedlings grown on Santa Lucia, Tangair, and Tangair/sand soils under high and low water stress. (SL-H = Santa Lucia, high water; SL-L = Santa Lucia, low water; T-H = Tangair, high water; T-L = Tangair, low water; T/S-H = Tangair/sand, high water; T/S-L = Tangair/sand, low water)

Figure 8. Relative yields expressed as total biomass of Artemisia californica and Pinus muricata seedlings grown on Santa Lucia, Tangair, and Tangair/sand soils under high and low water stress. (SL-H = Santa Lucia, high water; SL-L = Santa Lucia, low water; T-H = Tangair, high water; T-L = Tangair, low water; T/S-H = Tangair/sand, high water; T/S-L = Tangair/sand, low water)

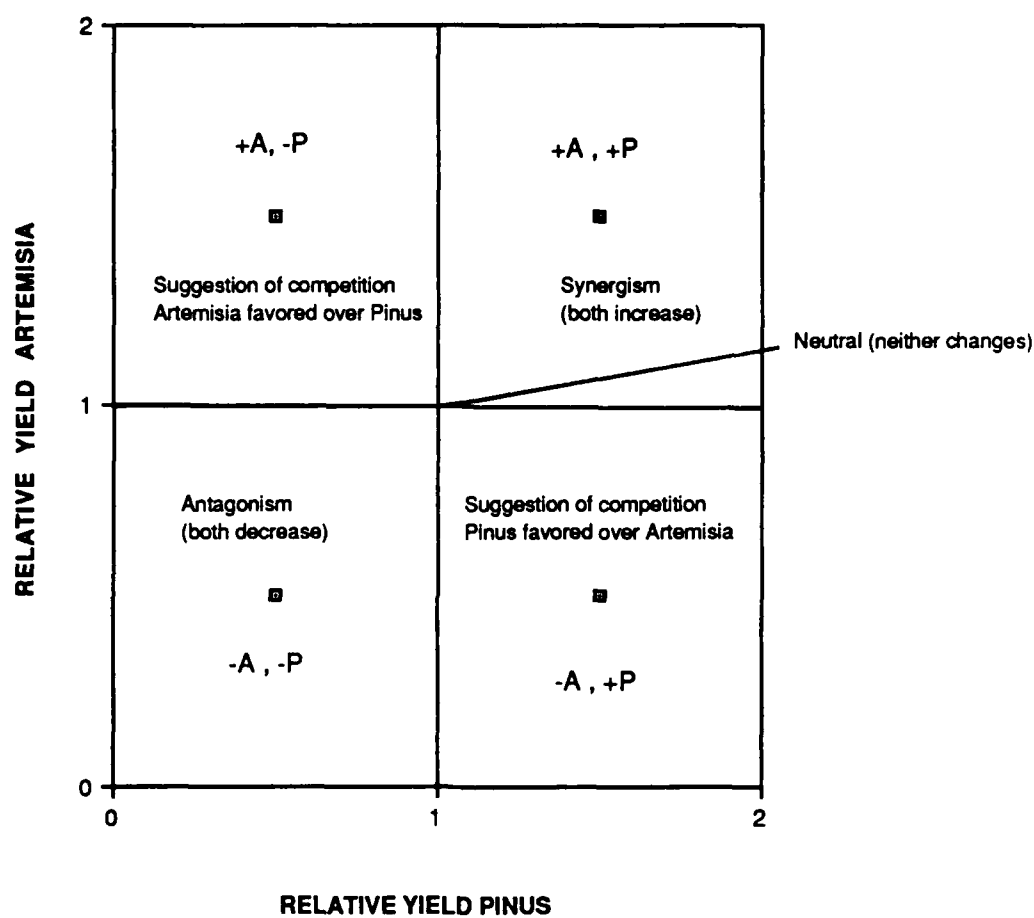


Fig. 1

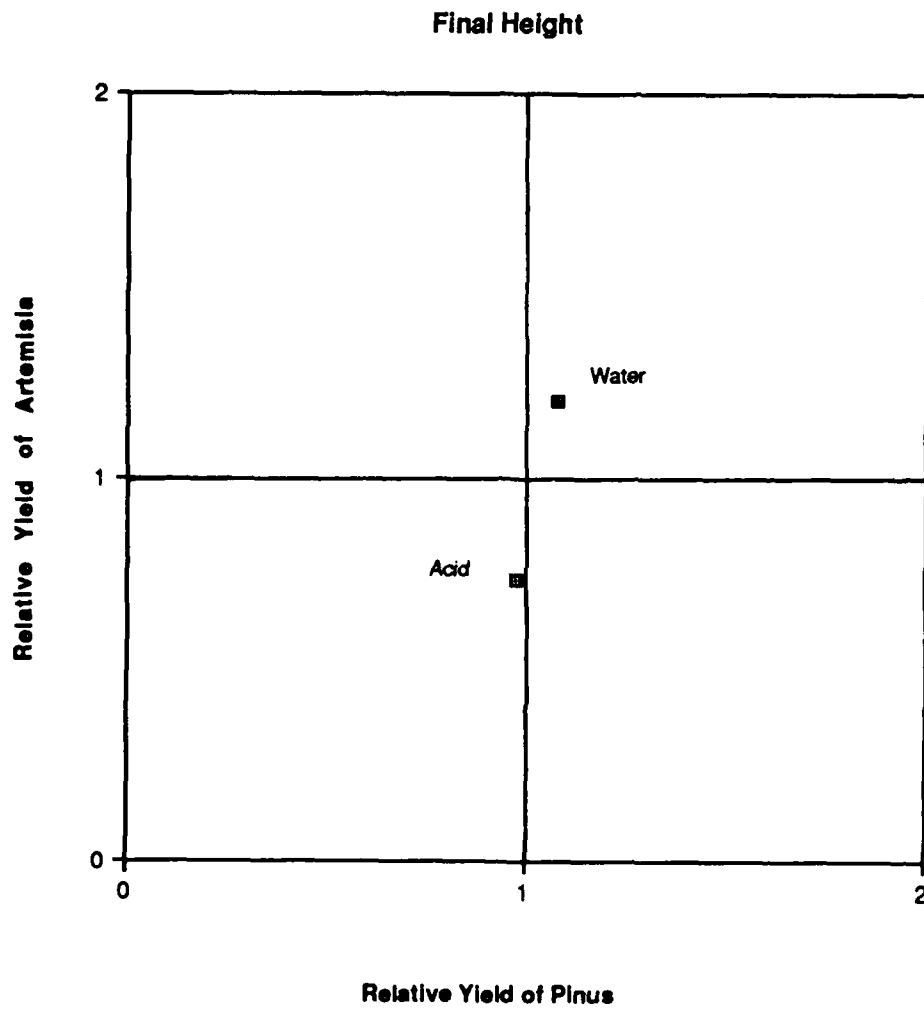


Fig. 2

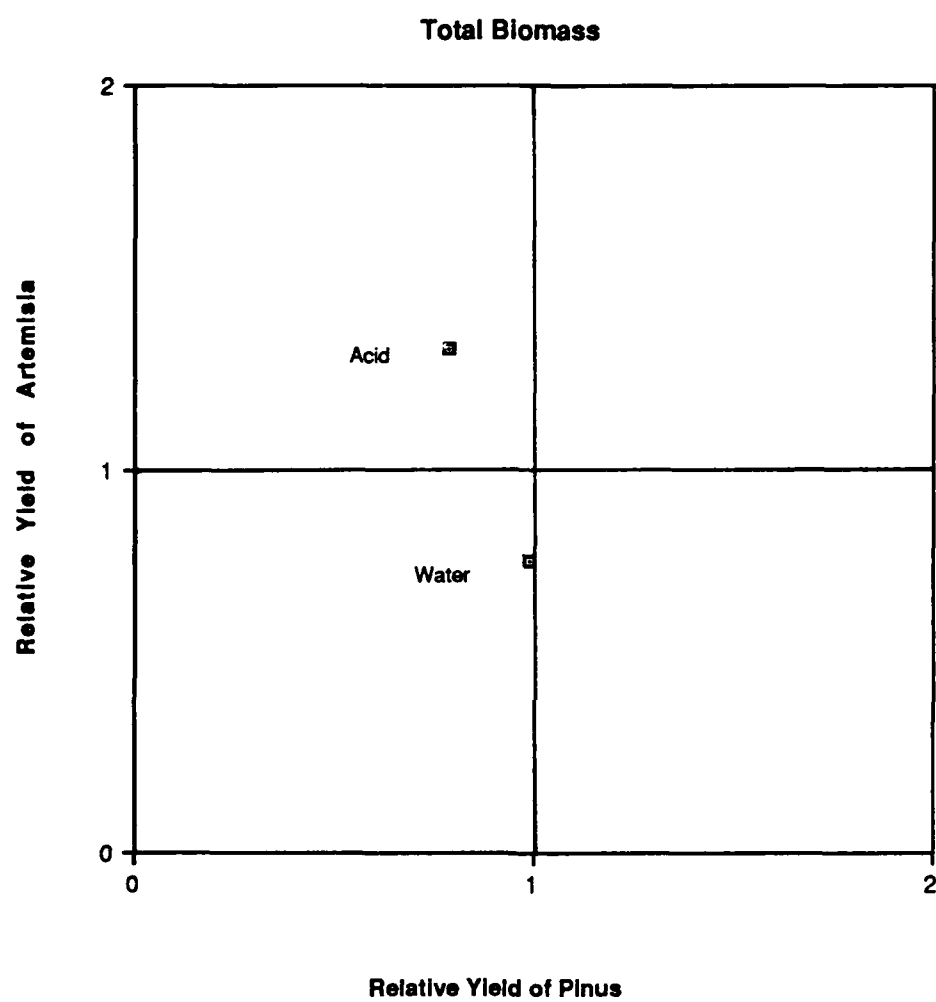


Fig. 3

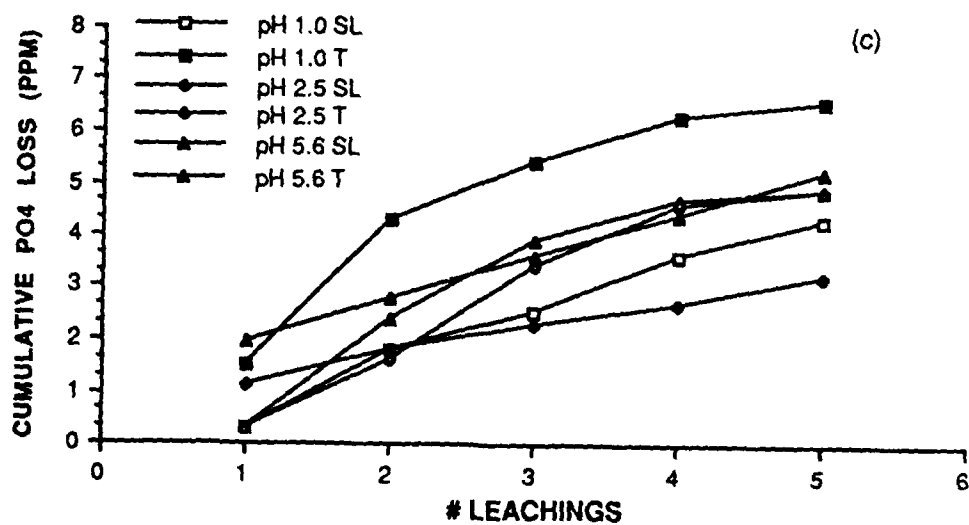
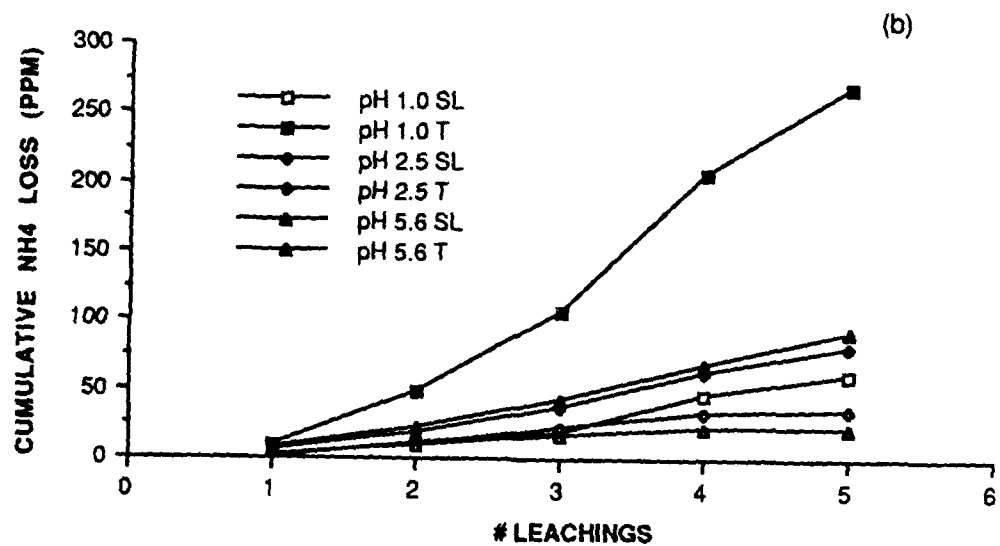
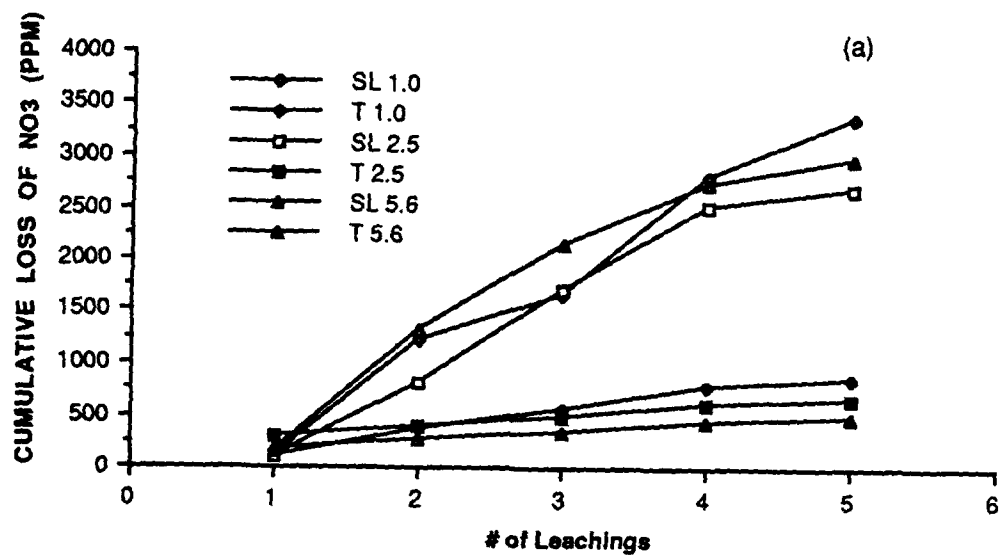


Fig. 4a-c

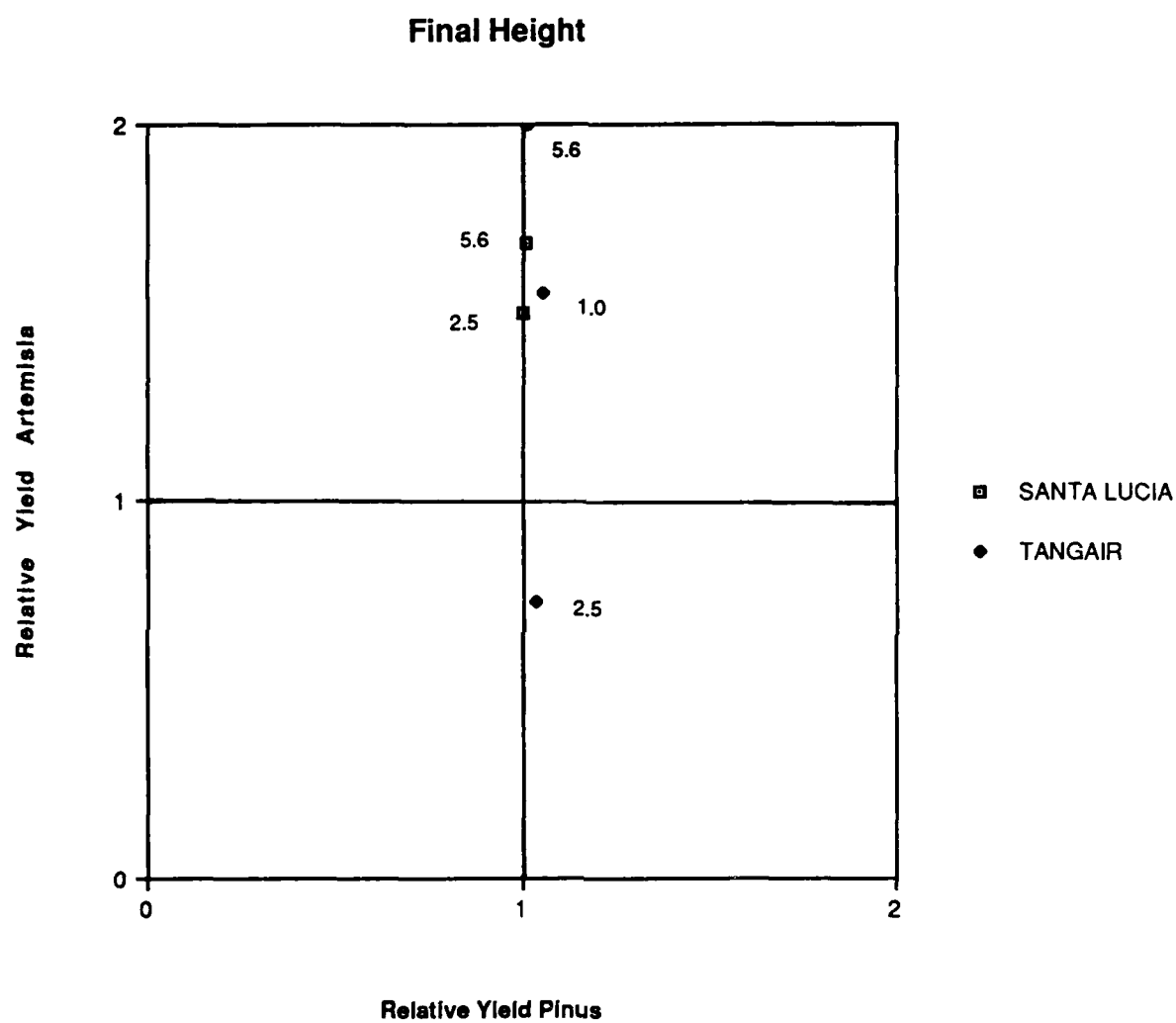


Fig. 5

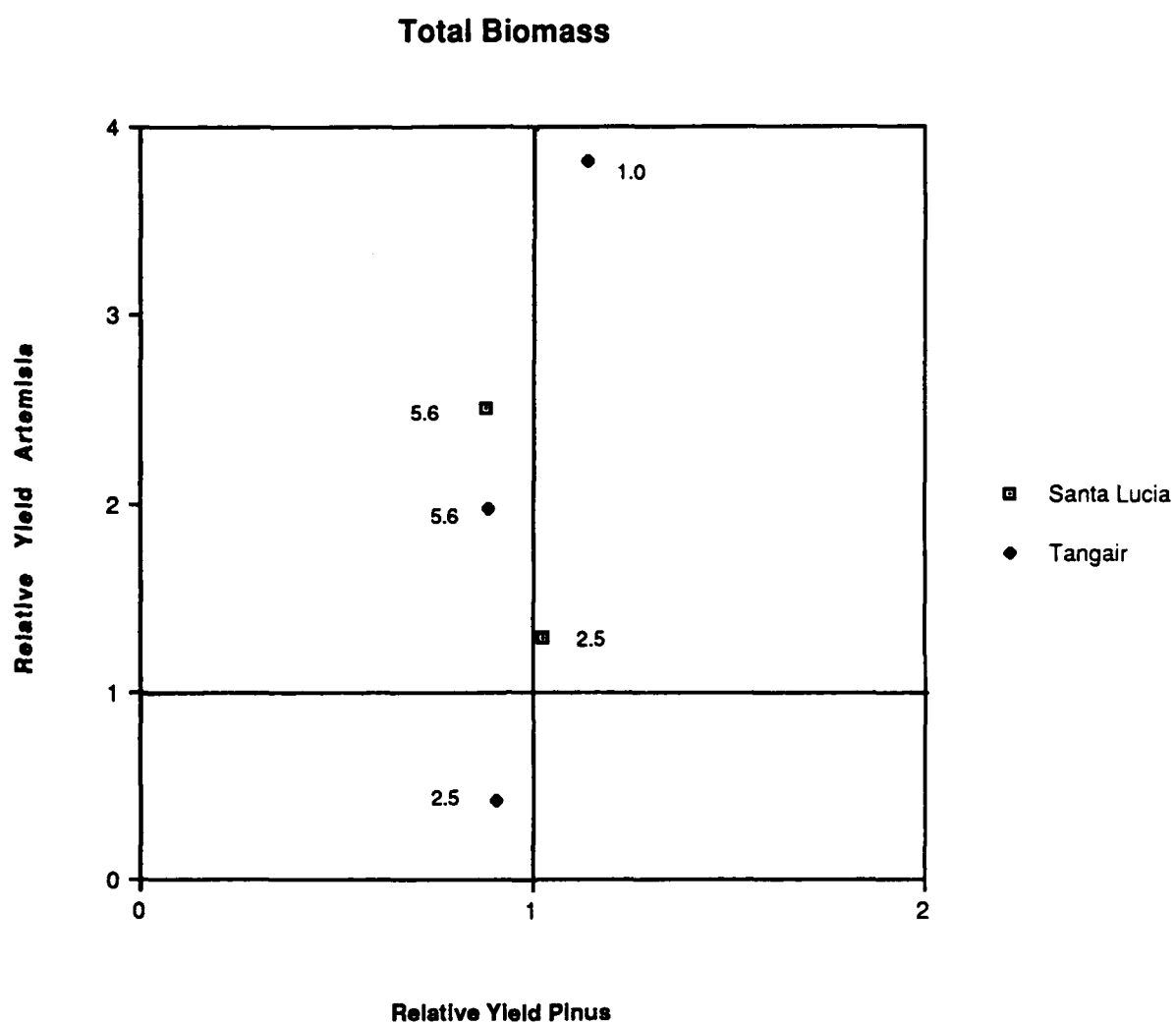


Fig. 6

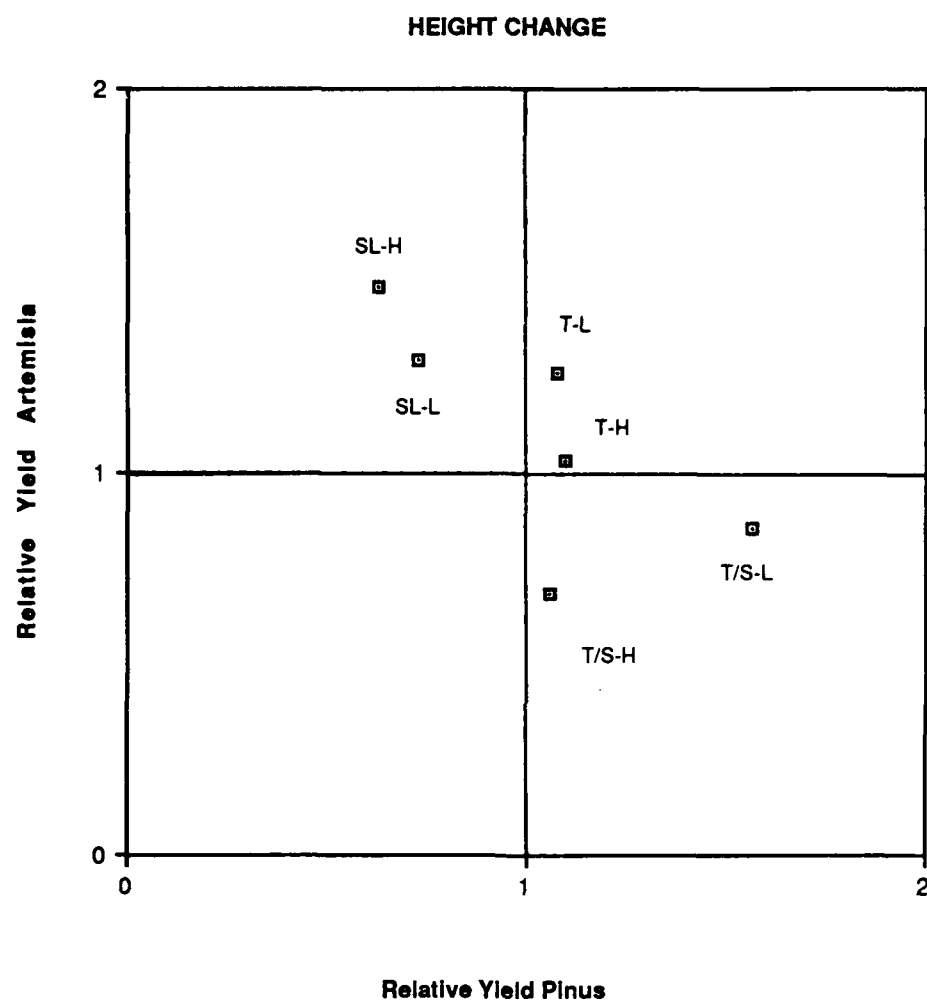


Fig. 7

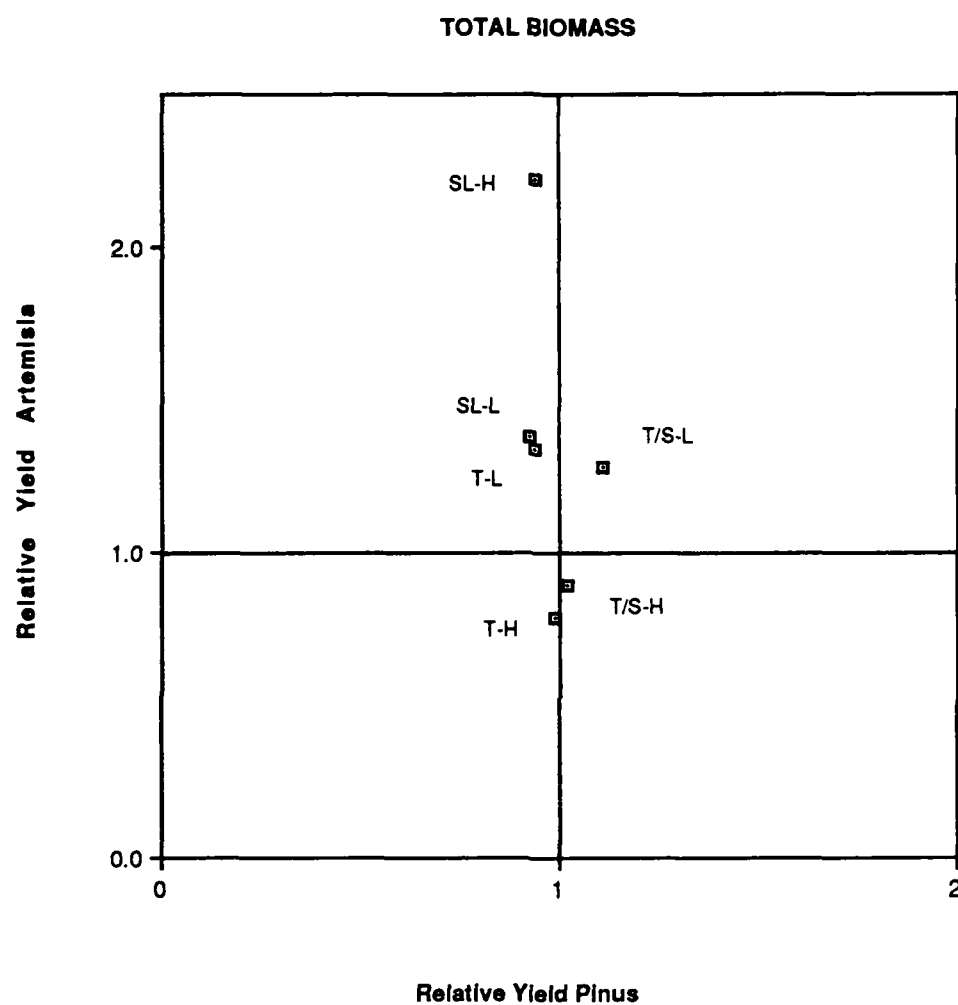


Fig. 8

PART 4

THE EFFECT OF EXTREME HYDROCHLORIC ACID DEPOSITION FOLLOWING
SIMULATED SHUTTLE ROCKET LAUNCHES ON SOIL CHEMICAL PROPERTIES

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ABSTRACT

The objective was to evaluate the effect of extreme hydrochloric acid (HCL) deposition following simulated shuttle rocket launches on soil chemical properties. Four soils along a soil chronosequence from Vandenberg Air Force Base were selected and evaluated as a function of pH spike additions (pH=1.0, 2.5, 4.0, and 5.6) and subsequent leaching by simulated rain. The major effects occurred in the pH=1.0 treatment; the higher pH treatments (pH=2.5, 4.0, and 5.6) behaved similarly. The pH=1.0 treatment led to a pH decrease to 2.5 in poorly buffered soils and increased leaching of bases (Ca, Mg, K, and Na) and Al. Acid buffering capacity increased with increasing soil age. Ammonification was increased and nitrification was decreased by the pH=1.0 treatment. It was hypothesized that acid neutralization involved reaction of protons with polyhydroxyl-Al complexes, base removal, clay acidification, and chemical weathering. The ultimate effect of extreme HCl deposition is podzolization, but ameliorative treatments and rocket launch meteorological specifications can prevent this problem.

INTRODUCTION

The literature on the effect of acid deposition on soils and plants is voluminous (Hutchinson and Havas 1980, Johnson et al. 1982, U.S. DOE 1983, Evans 1984, Morrison 1984). The majority of work has centered on nitric and sulfuric acids because these are the principal acidic components of most acid precipitation. Less attention has centered on hydrochloric acid even though the chloride ion is very mobile and should be highly effective in leaching bases from soils (Wiklander 1980, Johnson et al. 1982).

Shuttle rocket launches produce 10^5 kg HCl below 4 km as a by-product of solid fuel ignition (Madsen 1981). Acid deposition rates in near-field environments are as high as 183 meq/m² with pH's ≤ 1.0 (NASA 1979, Milligan and Hubbard 1983, Pellett et al. 1983). These high acid deposition rates have resulted in plant death, plant compositional changes, and fish kill (Milligan and Hubbard 1983, Potter 1983). Recent work has shown that seed germination and seedling growth of native plant species are severely affected by single soil applications of pH=1.0 HCl (Zammit and Zedler 1988). There are a number of potential proton (H^+ ion) sinks in soils (Ulrich 1980, Van Breemen et al. 1984, Reuss and Johnson 1986). The relative importance of these proton sinks on extreme HCl leaching is unknown.

The objective of this study was to assess the effects of extreme HCl deposition on soil chemical properties particularly with respect to the soil as a medium for plant growth. The major idea was to add acid to the soil under conditions which simulate a shuttle rocket launch. The soils for this study were collected along a soil chronosequence on Vandenberg Air Force Base (VAFB) in California, the site of a new shuttle rocket launch site. The soils were collected along a soil chronosequence to test the hypothesis that: soil resistance to acid deposition will increase with increasing soil age.

METHODS AND MATERIALS

The Experimental Site and Soils

The experimental site is on the Vandenberg Air Force Base (VAFB) near Lompoc, California (N 34° 37', W 120° 37'). The mean annual temperature and precipitation

for VAFB are 13 °C and 323 mm, respectively. Soils were collected along a topographic transect from the ocean into the foothills just north of Point Pedernales and represent four soil types: Dune Sand, Baywood, Tangair, and Santa Lucia soils (Cole et al. 1958). The first three soils are derived from marine sands and the Santa Lucia soil is derived from shale. The Baywood soil is an Entic Haploxeroll (sandy, mixed, thermic); the Tangair soil is a Typic Psammaquent (mixed, mesic); and the Santa Lucia soil is a Pachic Ultic Haploxeroll (clayey-skeletal, mixed, thermic) (Shipman 1972, Shipman 1980). The Dune Sand is called Dune Land in more recent soil surveys and is not classified with respect to the 7th Approximation.

Because of the topographic positioning, these soils are thought to represent a soil chronosequence with Dune Sand as the youngest and Santa Lucia as the oldest end-members. Justification for considering these soils as a chronosequence will be given in the Results.

Vegetation on the Dune Sand area consist mainly of drought deciduous shrubs (Lupinus chamissonis, Artemisia californica) and the evergreen species, Haplopappus ericoides. The vegetation on the Baywood soil is a well-developed coastal sage-scrub dominated by the drought-deciduous Artemisia californica and the evergreen Haplopappus ericoides. Some sub-shrubs (Lotus scoparius) and herbs (Scrophularia atrata) are also abundant. In the lower zone of the Tangair area, the typical vegetation is coastal sage-scrub and is dominated by Baccharis pilularis, Lotus scoparius, and Rubus ursinus. Artemisia californica and Salvia mellifera are also conspicuous. In the upper zone of the Tangair area, the typical vegetation is hard chapparal dominated by Ceanothus thrysiflorus, Ceanothus impressus, Rhamnus californica, and Salvia mellifera. The Santa Lucia site supports both sage-scrub type vegetation (Salvia mellifera, Artemisia californica, and Bacharis pilularis) and

chaparral vegetation (Adenostoma fasciculatum, Ceanothus ramulosus, and Arctostaphylos pechoensis).

Soil Processing and Analysis

Within each soil type, five soil pits were excavated and sampled by soil horizon down to 1.0 m or bedrock. Soil samples were taken by volume and used to calculate bulk density. Within the Santa Lucia soil area, there were pockets of deep soil surrounded by the more common shallow soil. Both the shallow and deep soil areas were sampled and described separately (Table 1). After sampling, soils were allowed to air-dry.

After air-drying, the soils were sieved to pass a 2 mm screen. All subsequent analyses were done on the air-dry, ≤ 2 mm fraction. A subsample of this fraction was oven-dried at 105 °C. All chemical analyses in this paper are reported on an oven-dry, ≤ 2 mm basis. Conversion of these chemical analyses to a field basis necessitates correcting for gravel (> 2 mm) content (Table 1).

Soil texture was measured with the hydrometer method (Day 1965). Soil pH was measured in both water and 0.01 M CaCl_2 (McLean 1982). Exchangeable bases (Ca, Mg, K, and Na) were measured by extraction with 1.0 M NH_4OAc (Thomas 1982). This base concentration was corrected for water soluble ions with a separate water extract. Total N was determined with a Kjeldahl procedure (Bremner and Mulvaney 1982). Total P was determined by perchloric acid digestion (Olsen and Sommers 1982). Total C was determined on a Leco carbon analyzer.

The leachate Ca, Mg, Na, and Al concentrations were measured with a Perkin-Elmer Model 6500 ICP emission spectrograph. Leachate K was measured with a Perkin-Elmer Model 306 atomic absorption spectrophotometer. Ammonium-N, NO₃-N, PO₄-P, and Si were measured colorimetrically using a Technicon Autoanalyzer. Leachate pH was measured with a Ross pH electrode and an Orion pH meter.

The Leaching Experiments

The leaching experiment used to assess the potential effects of HCl deposition on soil chemical properties was designed to simulate the environment and technical aspects of shuttle launches at VAFB. Only the surface soil horizons (Table 1) were used in the leaching experiments. A total of 80 soil samples (4 soils x 4 pH values x 5 replicates) plus 12 blanks were analyzed. Fifty g of air-dry soil were placed in Falcon 150 ml filter units. Five ml of HCl solution (the "spike") were dispensed on the soil, allowed to sit overnight, and extracted under vacuum (0.01 MPa) the following day with 100 ml of deionized water. Leachate samples were refrigerated and analyzed promptly. The soils were placed in a 13 °C incubator and incubated for 1.0 month and then re-extracted. A total of five extractions over a 4 month period were analyzed.

The HCl acid solutions were prepared by titrating deionized water with HCl to the required endpoints (1.0, 2.5, 4.0, and 5.6) as judged with a pH electrode. The acid loading of the pH=1.0 treatment was of particular interest because it represented an extreme condition and the amount of this acid added to the soils was similar in magnitude to the exchangeable bases. Unfortunately, the concentration of the pH=1.0 solution was never measured. The theoretical concentration of a pH=1.0 solution is 0.127 meq/l (Robinson and Stokes 1970) However our solution was

prepared by titration outside the range of buffer solutions (pH 2-5). An alternative method for estimating the concentration of this solution is to utilize the blank solution data. For the first four extractions, the blank solution (5 ml of acid + 100 ml of water, 21-fold dilution) mean pH was 2.20 ± 0.03 . For the final extraction, the blank solution (5 ml of acid + 150 ml of water, 31-fold dilution) mean pH was 2.38 ± 0.01 . By successive approximations, one can estimate ionic strength, activity coefficients, and the concentration of the H^+ ion as outlined in the following section. The H^+ ion concentration using the 21-fold and 31-fold concentration data were 0.144 and 0.138 meq/l, respectively. Since these numbers were determined from solutions within the range of buffer standards, they are probably more accurate than the theoretical concentration of the pH=1.0 solution. For this paper, the H^+ ion concentration of the pH=1.0 solution was assumed to be 0.141 meq/l.

The reasons for the experimental configuration are as follows. The HCl deposition associated with shuttle launches is episodic. One month is probably a minimum time between successive shuttle launches. We wanted to simulate this monthly interval in order to allow the soil time to rebound from HCl deposition especially with respect to microbial activity and mineral dissolution. Five ml of pH=1.0 solution contains 0.705 meq H^+ ion. Given the configuration of the incubation chamber, this is equivalent to 189 meq/m² which is close to reported rates of deposition at Kennedy Space Center both with respect to quantity (183 meq/m²) and quality (pH=1.0) (Milligan and Hubbard 1983, Madsen 1981, Pellett et al. 1983). The leaching with 100 ml of deionized water is equivalent to 26.8 mm of rain which is close to the mean monthly precipitation at VAFB of 26.9mm. The incubation temperature of 13°C is the mean annual temperature at VAFB. The spike solution pH values of 1.0, 2.5, 4.0, and 5.6 were chosen in order to simulate the entire range of probable acidic deposition following shuttle launches.

Solution Phase Activity Calculations

Solution phase activities were calculated except for H^+ activity which was directly measured. The activity (a) of a chemical species is defined by:

$$a = \gamma c \quad (1)$$

where γ is the activity coefficient and c is the molar concentration. Activity coefficients were determined with the Davies equation:

$$\log(\gamma) = -Az^2((\sqrt{I}(1.0 + \sqrt{I}) - 0.3I) \quad (2)$$

(Sposito 1981) where A is a constant, z is the valence and I is the ionic strength defined as:

$$I = 0.5 \sum c_i z_i^2 \quad (3)$$

Activity coefficients of neutral chemical species were assumed to be unity. The assumption was made that the principal soluble cations were H , Al , Ca , Mg , K , and Na which were balanced by Cl (not measured). Because the Cl anion forms only weak ion-pairs (Lindsay 1979), ion-pairing was ignored. Aluminum was assumed to exist as a series of monomers in solution:



Given measurements of Al_t , the dissociation constants for the aluminum hydroxide monomers (Lindsay 1979), and the ionic strength, one can solve for the concentration and activity of the individual ions in solution. A computer program was written to solve, by successive approximations, for the Al species and to ascertain the H^+ ion concentration in solution. The latter was needed for estimating the molar flux of H^+ ions through the soils. Input to the program included pH, Ca, Mg, K, Na, and Al_t concentrations. Silicon was assumed to exist entirely as the undissociated silicic acid (H_4SiO_4).

The uncertainties involved in this solution phase model are greatest for Al. Recent work suggest that complex Al polymers and organic Al complexes are important constituents of the solution phase under natural conditions (Ulrich 1980, Johnson et al. 1981). The latter complexes were ignored in our model for lack of experimental data. However, under the very acid conditions ($pH < 3.0$) which developed in the latter phases of our leaching experiments, the dominant Al species in solution is clearly Al^{3+} . At least under these conditions, the model should be valid.

Statistical Analyses

The solution phase chemical extract data were analyzed with a three factor factorial analysis of variance (ANOVA). The factors were soil type (Dune Sand, Baywood, Tangair, and Santa Lucia), pH spike (1.0, 2.5, 4.0, 5.6), and time (0, 1, 2, 3, and 4 months). Soil and pH were handled as grouping factors and time as a trial factor in a repeated measures design. There were five replicates of each of the 16 soil-pH combinations. The statistical analyses were done using the BMDP programs (Dixon and Brown 1979). Tukey's honestly significant difference (hsd) test was used to test for differences among treatment means (Steel and Torrie 1960).

RESULTS

The Soil Chronosequence

Based on position within the landscape, it was hypothesized that the soil toposequence was also a soil chronosequence. Soil bases and total carbon within the surface meter of soil increase across the hypothesized chronosequence (Fig. 1). These results strongly support the chronosequence hypothesis. However, because the Santa Lucia soil is formed on a different parent material (shale) from the other soils (sand), it is not possible to attribute the differences between the Santa Lucia and the other soils to time exclusively. Nevertheless, the total carbon and bases in the Santa Lucia soil follow the trend expected for a chronosequence; therefore, in the subsequent analysis, this transect will be referred to as the soil chronosequence and results will be presented along this soil sequence.

The Statistical Analyses

In general, the factorial ANOVA found significant main effects (soil, pH spike, and time) as well as significant interaction terms (Table 2). The elements which showed the weakest relationship to the main treatment variables were Na and $\text{NO}_3\text{-N}$, two elements which are weakly adsorbed and readily lost through leaching. An analysis of the soil x pH interaction generally showed a significant difference between the pH=1.0 treatment and the remaining pH treatments (Table 3). The pH was significantly depressed and the concentrations of Ca, Mg, K, Na, Al, Si, and $\text{NH}_4\text{-N}$ were significantly increased. The pH=1.0 spike had a major influence on leaching

of most elements. As our ANOVA table demonstrated (Table 2), time was also a critical factor.

Seven selected variables (pH, Ca, K, $\text{NO}_3\text{-N}$, $\text{PO}_4\text{-P}$, Si, and Al) will be used to demonstrate the effect of time. Soil pH dropped to < 3.0 with one spike of $\text{pH}=1.0$ solution for the Dune Sand soil (Fig. 2). The remaining soils showed greater resistance to pH change and in the order hypothesized for the chronosequence: Dune Sand $<$ Baywood $<$ Tangair $<$ Santa Lucia. The extract pH was generally lower for the $\text{pH}=2.5$ spike than for the $\text{pH}=4.0$ and the $\text{pH}=5.6$ spikes but not in all cases (Fig. 2).

The $\text{pH}=1.0$ spike led to a rapid depletion of both Ca and K especially from the Dune Sand, Baywood, and Tangair soil (Figs. 3 and 4). Only the Santa Lucia soil showed no obvious trend toward depletion of Ca and K. As was the case for pH, the trends in the Ca and K data for $\text{pH}=2.5$, 4.0, and 5.6 spikes are similar. Only the $\text{pH}=1.0$ spike showed significant differences.

Nitrogen and P are the two essential plant elements that most frequently limit terrestrial plant growth. As such they were of particular importance in assessing the effect of HCl deposition on the soil as a medium for plant growth. In general, the $\text{pH}=1.0$ spike led to a significant increase in the concentration of $\text{NH}_4\text{-N}$ in the extracts (Table 3). In contrast, there was a decrease in $\text{NO}_3\text{-N}$ concentrations (Fig. 5). For both the Dune Sand and Baywood soils, $\text{NO}_3\text{-N}$ levels fell to zero on the third extraction (2 months). The pH lowering depressed the bacterially mediated nitrification process. The $\text{pH}=2.5$, 4.0, and 5.6 spikes followed similar time trends. The rate of nitrification increased with increasing soil age. The major effect of HCl addition on $\text{PO}_4\text{-P}$ was to increase the concentration in the $\text{pH}=1.0$ spike in the Dune

Sand soil (Table 3, Fig. 6). This increased concentration is probably due to the highly acidic concentration of the Dune Sand soil (Fig. 2); however, it is unclear why the Baywood soil did not respond in a similar way once the pH dropped.

Silicon and Al were included in this study because they should reflect mineral weathering, a potentially important process in acid neutralization. The pH=1.0 spike increased dramatically the leaching of Si from the Dune Sand, Baywood, and Tangair soils (Fig. 7). The effect of the pH=1.0 spike was less pronounced for the Santa Lucia soil only because the Santa Lucia soil Si concentrations were high across all pH treatments (Fig. 7). This difference in Si solubility among soils is attributable to a difference in parent material. The parent material for Dune Sand, Baywood, and Tangair soils is marine sand, while the parent material for the Santa Lucia soil is siliceous or diatomaceous shales of the Monterey formation (Cole et al. 1958). Aluminum concentrations paralleled pH (cf. Figs. 2 and 8). Aluminum concentrations were substantially above background levels only where the extract pH was < 4.0. Aluminum is important not only because it affects the acid neutralization process, but also because Al is toxic to plant growth. Concentrations as low as 37 mmol/l (1.0 mg/l) can be toxic to sensitive plants (Pratt 1966). However there is considerable variation in plant sensitivity to Al including evidence that some forest trees can withstand Al concentration > 2000 mmol/l (Johnson et al. 1982, Morrison 1984). Only where the pH was < 4.0 were concentrations of Al in the range that could prove toxic to plants (Table 3, Fig. 8).

System Inputs and Outputs

The distribution of charge-carrying cations in the leachates was ascertained using the successive approximations technique previously described. Soil bases were rapidly

leached from the Dune Sand and Baywood soils (Fig. 9); at the conclusion of the experiments, the dominant cations were the acidic Al and H ions. On the other hand, at the conclusion of the experiments, the Tangair soil was approximately balanced between basic and acidic cations; acidic cations only carried a minor amount of the charge in the base-rich Santa Lucia soil.

The acid addition (input) to the soils varied from 14.3 (Tangair) to 15.8 (Dune Sand) meq/kg soil. The slight variation in acid addition is due to a slight difference in the moisture content of the air-dry experimental soil. The experimentally measured outputs varied from 16.2 to 17.7 meq/kg soil (Fig. 9). The system output was higher by a consistent amount (1.7 ± 0.3 meq/kg) from the system input for all four soils. There are a number of possible explanations for this discrepancy. One, the indirect method used to calculate input H concentration could be in error (See Methods and Materials). Two, non-stoichiometric reactions involving mineral dissolution could be taking place. Three, there could be errors in the analytical determinations. And four, there could be errors in the calculation of the output Al and H ion concentrations by the successive approximations technique. Following the first extraction when considerable solution was retained by the initially air-dry soil, there was a consistent level of extracted charge in spite of the fact that the charge-carrying cations changed significantly (Fig. 9); this would argue in favor of minor errors in either analytical measurements or calculation of H and Al output concentrations. Also there was a consistent difference between the system input and output for each soil (1.7 ± 0.3 meq/kg); this consistency suggests an error in the calculation of the input H concentration as the most likely explanation for the discrepancy between input and output. Whatever the cause, the magnitude of this discrepancy (ca. 10%) is insufficient to alter the main conclusions with respect to the dominance of basic and acidic ions as charge carriers.

A comparison of extracted and exchangeable bases shows an approximate balance to slight excess of extracted bases except for the Santa Lucia soil where a considerable residual of exchangeable bases remained in the soils at the conclusion of the experiments (Fig. 10). For the Dune Sand and the Baywood soils despite the acid additions considerable in excess of soil base content, there still remained at the conclusion of the experiments a small amount of base removal which suggest mineral dissolution (Fig. 9). For the Dune Sand and Baywood soils, the base-Al-H ratios of the extracts for the last two extraction appear to have reached constant ratios which suggests that the soils may have reached a temporary steady-state.

Mineral Solubility

For comparative purposes, the solubility products of a few common soil minerals are plotted along with calculated solution phase activities (Fig. 11). The solubility of Si in the Santa Lucia soil is quite independent of pH or Al concentration and falls between the solubility of "soil-Si" and quartz, the most stable silica mineral (Lindsay 1979). The solubility of Si in the Santa Lucia soil is probably not governed by an aluminosilicate mineral. On the other hand at high pH, the possibility exists that an aluminosilicate mineral is governing the solubility in the other soils as the trend in the data follows that of kaolinite (Fig. 11). Also, the data roughly follow gibbsite solubility. However this relationship breaks down at low pH which can be most easily seen by plotting pAl versus pH directly (Fig. 12). Above pH 4.5, the gibbsite solubility line fits the data very well; below pH 4.5, the relationship breaks down. On the other hand, a straight line fits the pAl versus pH data across the entire pH range (Fig. 12). The relationship between Al and pH is critically important because

Al chemistry has been directly linked to the soil acid neutralization process (Ulrich 1980, Johnson et al. 1981).

DISCUSSION

The Acid Neutralization Process

A number of mechanisms could be responsible for proton removal in the experimental soils including ion-exchange, protonation of anions, and mineral weathering (Van Breemen et al. 1984). There is evidence that the acid neutralization process is not due to a direct exchange of protons for basic cations on the exchange complex. Clay mineralogists have known for years that it is difficult, if not impossible, to produce H^+ saturated clays; invariably a H-Al clay is produced (Grim 1968).

Any mechanism for describing the acid neutralization process must be able to account for both base displacement and solubilization of Al since Al is known to be involved in the acid neutralization process. A mechanism which can account for these properties assumes that protons are neutralized by polyhydroxyl-Al complexes associated with clay minerals (Fig. 13). Protons are neutralized by OH ions forming water; associated with this change is the acquisition of a positive charge by the aluminum complex and as a consequence, the displacement of a basic cation. This acid neutralization process continues until the entire polyhydroxyl-Al complex is converted into Al^{3+} ions. According to this model (from Bohn et al. 1985), Al^{3+} should only be significant below pH 4.5, which agrees with our experimental results at least for the sandy soils (cf., Figs. 2 and 8). In the Santa Lucia soil (shale-derived), the Al concentrations in the pH=1.0 spike treatment never increased above levels

for the other pH treatments even though the extract pH fell to slightly below 4.0. The high residual base content of the Santa Lucia soil at the conclusion of the experiments (Fig. 10) may account for the low Al solubility since Al is strongly adsorbed by soils. These reactive polyhydroxyl-Al complexes are important in several phenomena outside the immediate scope of this paper including pH-dependent cation exchange capacity (Bohn et al. 1985) and sulfate adsorption (Johnson 1980).

The proposed model is similar to those proposed by Bohn et al. (1985) to account for pH dependent charge and that proposed by Ulrich (1980) to account for acid neutralization. Johnson et al. (1981) proposed a two step model to account for acid neutralization at Hubbard Brook. The two steps were : (1) H^+ ion is neutralized by dissolution of reactive alumina and (2) H and Al acidity is neutralized by chemical weathering of primary minerals. In their work, they hypothesized based on solubility measurements that the reactive alumina was a gibbsite-like mineral ($Al(OH)_3$). Based on our solubility measurements, an argument can be made that their model also fits our data. Above pH 4.5, Al solubility is governed by gibbsite (Fig. 12) and the acid is neutralized by dissolution of gibbsite; if we assume that the strongly adsorbed trivalent Al ion is adsorbed onto the clay mineral displacing basic cations which subsequently leach, then we have a mechanism almost identical to that proposed here (Fig. 13). In fact, there is no way to distinguish these two mechanisms based on the reported solubility data.

However, from our work, it is clear that a gibbsite-like mineral is not responsible for Al solubility at $pH < 4.5$; the concentration of Al under very acidic conditions ($pH < 3.0$) is much less than that supported by gibbsite (Fig. 12). Also, the strong correlation between pAl and pH across the entire range suggests a single mechanism

(Fig. 12). Furthermore, Ulrich (1980) claims that gibbsite is missing in most acid soils. The assumption that the "reactive alumina" is a polyhydroxyl-Al complex is more in keeping with both solution and solid phase evidence (Ulrich 1980, Bohn et al. 1985).

Three pieces of evidence suggest that some mineral dissolution (chemical weathering) occurred. The pH of the soil extracts for the last two samplings of the Dune Sand and Baywood soils were consistently higher by 0.15 ± 0.04 pH units than a blank. That is, these soils never reached the point where the pH of the input solution (assumed to be the same as the blank) became equal to the pH of the output (extract) solution. A 0.15 pH difference can account for neutralization of about 29 % of the H^+ ion input. The continuing base extraction in the Dune Sand and Baywood soils at the end of the experiments also supports the argument that chemical weathering was taking place (Fig. 9). The slight excess of Ca and K in the extracts relative to exchangeable bases (Fig. 10) also suggests chemical weathering.

A four step mechanism is proposed to account for acid neutralization, base exchange, and Al solubility under our experimental conditions. One, acid is neutralized by reaction with reactive alumina (polyhydroxyl-Al complexes) associated with the exchange complex. Two, as reactive alumina acquires charge, bases are displaced. Three, eventually a pure acidic (H-Al) clay develops. And four, further acid neutralization is governed by chemical weathering via the acidic cations (H^+ , Al^{3+}).

The Soil as a Medium for Plant Growth

Of the HCl treatments evaluated, only the pH=1.0 spike had a profound effect on soil chemical properties. The pH=1.0 treatment led to a significant decrease in soil pH; accompanying this pH decrease was a significant loss of exchangeable bases and a significant increase in Al solubility. Soil ammonification was increased and soil nitrification was decreased by the pH=1.0 treatment. Soil acidification increased P leaching only for the Dune Sand soil which was the most poorly buffered soil.

The loss of exchangeable bases, decrease in soil pH to 2.5, and increase in Al concentrations to possibly toxic concentrations are all adverse effects on the soil as a medium for plant growth. However, to place these results in perspective, it is necessary to quantify these effects relative to field conditions. To do this, an estimate was made of the number of HCl additions (183 meq/m^2 , a measured Kennedy Space Center input) that it would take to remove the bases from the soils (Fig. 14). This calculation considers bulk density, depth of soil horizons, exchangeable base content, and gravel content (Table 1). Fifty additions of acid would be sufficient to leach the bases from the surface meter of soil for the Dune Sand soil. On the other hand, 100 additions of acid would only leach the bases from the surface 16 cm of the Santa Lucia soil. However, there was both a shallow and deep phase for the Santa Lucia soil (Table 1). For the shallow phase soil, 16 cm is 64% of the soil depth. Loss of 64% of the bases is significant. The resistance to change as judged by base removal was directly related to soil age as was hypothesized initially. The older the soil, the greater the resistance to acidification.

There was evidence for both exchangeable base removal and chemical weathering. Although it appears that chemical weathering may be in a steady-state at present,

ultimately, these minerals will also be removed from the soil profile. Base removal coupled with removal of primary and secondary minerals from the soil profile under intense acidic leaching is a well-known process in soils and is called podzolization (Norton 1976). The ultimate effect of intense acidic leaching is a soil devoid of organic matter, minerals, and exchangeable bases, low in pH, high in Al, and low in soil fertility.

Fortunately, the case considered (Fig. 14) is a worse-case scenario which assumed repeated additions to the same point on the soil surface. The actual deposition depends on meteorological conditions at launch time. The worse condition for acid deposition is a rain storm immediately after launch which brings the acid down in a small area; with no rain, the acid deposition is dissipated over a wider area. Also, winds which blow the acid-laden clouds to sea minimize acidic damage because ocean waters are alkaline ($\text{pH}=7.9$, alkalinity = 230 meq/l (Stumm and Morgan 1970)) and can easily absorb the acid. For example, 100 additions of acid (183 meq/m^2) would neutralize about 8.0 cm of ocean water. Given the mixing of ocean waters, this is a minor effect. It is possible to treat the worse affected terrestrial areas by application of bases (e.g., CaCO_3) to the soil surfaces to neutralize the acid. A more difficult immediate problem is the effect of acidic deposition on plant composition. A plant compositional change seems inevitable (Potter 1983).

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LITERATURE CITED

- Bohn, H.L., McNeal, B.L., and O'Connor, G.A.: 1985, *Soil Chemistry* (2nd Ed.), J. Wiley & Sons, New York.
- Bremner, J.M. and Mulvaney, C.S.: 1982, Chapter 31, Nitrogen-Total, In: Page, A.L., Miller, R.H., and Keeney, D.R. (eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties* (2nd Ed.), American Society of Agronomy, Madison, Wisconsin, p. 595-624.
- Cole, R.C., Gardner, R.A., Gowans, K.D., Begg, E.L., Huntington, G.L., and Leifer, L.C.: 1958, *Soil Survey of the Santa Barbara Area, California*, United States Department of Agriculture, Washington, D.C.
- Day, P.R.: 1965, Chapter 43, Particle Fractionation and Particle-Size Analysis, In: Black, C.A. (ed.), *Methods of Soil Analysis, Part 1, Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling*, American Society of Agronomy, Madison, Wisconsin, p. 545-567.
- Dixon, W.J. and Brown, M.B.: 1979, *BMDP-79, Biomedical Computer Programs, P-Series*, University of California Press, Berkeley, California.
- Evans, L.S.: 1984, Acidic precipitation effects on terrestrial vegetation, *Ann. Rev. Phytopathol.*, 22:397-420.
- Grim, R.E.: 1968, *Clay Mineralogy* (2nd Ed.), McGraw-Hill Book Company, New York.
- Hutchinson, T.C. and Havas, M. (eds.): 1980, *Effects of Acid Precipitation on Terrestrial Ecosystems*, Plenum Press, New York.
- Johnson, D.W.: 1980, Site susceptibility to leaching by H_2SO_4 in acid rainfall, In: Hutchinson, T.C. and Havas, M. (eds.), *Effects of Acid Precipitation on Terrestrial Ecosystems*, Plenum Press, New York, p. 525-535.

- Johnson, D.W., Turner, J. and Kelly, J.M.: 1982, The effects of acid rain on forest nutrient status, *Water Resour. Res.*, 18:449-461.
- Johnson, N.M., Driscoll, C.T., and Eaton, J.S.: 1981, Acid rain, dissolved aluminum and chemical weathering at the Hubbard Brook Experimental Forest, New Hampshire, *Geochim. Cosmochim. Acta*, 45:1421-1437.
- Lindsay, W.L.: 1979, *Chemical Equilibria in Soils*, John Wiley & Sons, New York.
- Madsen, B.C.: 1981, Acid rain at Kennedy Space Center, Florida: recent observations, *Atmos. Environ.*, 15: 853-862.
- McLean, E.O.: 1982, Chapter 12, Soil pH and Lime Requirement, In: Page, A.L., Miller, R.H., and Keeney, D.R. (eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties*(2nd Ed.), American Society of Agronomy, Madison, Wisconsin, p. 199-224.
- Milligan, J.E. and Hubbard, G.B.: 1983, Near field biological effects of STS launches, *AIAA Shuttle Environment and Operations Meetings, Collection of Tech. Papers*, Washington, D.C., p. 101-103.
- Morrison, I.K.: 1984, Acid rain. A review of literature on acid deposition effects in forest ecosystems, *For. Abstracts*, 45:483-506.
- NASA: 1979, Kennedy Space Center, Final Environmental Impact Statement, National Aeronautics and Space Administration, JFK Space Center, Florida.
- Norton, S.A.: 1976, Changes in chemical processes in soils caused by acid precipitation, *Water, Air, Soil Pollut.*, 7:389-399.
- Olsen, S.R. and Sommers, L.E.: 1982, Chapter 24, Phosphorus, In: Page, A.L., Miller, R.H., and Keeney, D.R. (eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties* (2nd Ed.), American Society of Agronomy, Madison, Wisconsin, p. 403-430.

- Pellett, G.L., Sebacher, D.I., Bendura, R.J. and Wornom, D.E.: 1983, HCl in rocket exhaust clouds: atmospheric dispersion, acid aerosol characteristics, and acid rain deposition, *J. Air Pollut. Control Assoc.*, 33:304-310.
- Potter, A. (ed.): 1983, *Space Shuttle Environmental Effects: The First Five Flights, Proceedings of a NASA-U.S. Air Force Review Meeting (December 1982)*, JFK Space Center, Florida.
- Pratt, P.F.: 1966, Chapter 1. Aluminum, In: Chapman, H.D. (ed.), *Diagnostic Criteria for Plants and Soils*, University of California, Berkeley, California, p. 3-12.
- Reuss, J.O. and Johnson, D.W.: 1986, *Acid Deposition and the Acidification of Soils and Waters*, Springer-Verlag, New York.
- Robinson, R.A. and Stokes, R.H.: 1970, *Electrolyte Solutions (2nd Ed., revised)*, Butterworths, London.
- Shipman, G.E.: 1972, *Soil Survey of the Northern Santa Barbara Area, California*, U.S. Department of Agriculture, Washington, D.C.
- Shipman, G.E.: 1980, *Soil Survey of Santa Barbara County, California, South Coastal Part*, U.S. Department of Agriculture, Washington, D.C.
- Sposito, G.: 1981, *The Thermodynamics of Soil Solutions*, Oxford University Press, New York.
- Steel, R.G.D. and Torrie, J.H.: 1960, *Principles and Procedures of Statistics*, McGraw-Hill Book Company, Inc., New York.
- Stumm W. and Morgan, J.J.: 1970, *Aquatic Chemistry*, Wiley-Interscience, New York.
- Thomas, G.W.: 1982, Chapter 9, Exchangeable Cations, In: Page, A.L., Miller, R.H., and Keeney, D.R. (eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties (2nd Ed.)*, American Society of Agronomy, Madison, Wisconsin, p. 159-165.

- Ulrich, B.: 1980, Production and consumption of hydrogen ions in the ecosphere, In: Hutchinson, T.C. and Havas, M. (eds.), *Effects of Acid Precipitation on Terrestrial Ecosystems*, Plenum Press, New York, p. 255-282.
- U.S. DOE: 1983, *Acid Precipitation, A Bibliography*, U.S. Department of Energy, Oak Ridge, Tennessee.
- Van Breemen, N., Driscoll, C.T., and Mulder, J.: 1984, Acidic deposition and internal proton sources in acidification of soils and waters, *Nature*, 307:599-604.
- Wiklander, L.: 1980, Interaction between cations and anions influencing adsorption and leaching, In: Hutchinson, T.C. and Havas, M. (eds.), *Effects of Acid Precipitation on Terrestrial Ecosystems*, Plenum Press, New York, p. 239-254.
- Zammit, C.A. and Zedler, P.H.: 1988, Germination response to extreme acidity: impact of simulated acid deposition from a single shuttle launch, *Environ. Exper. Bot.*, 28:73-81.

Table II A summary of the significance levels (NS = nonsignificant, * = 5%, ** = 1%) of the experimental factors evaluated with a three-way ANOVA.

Experimental Factor	Extract Chemical Concentration									
	pH	Ca	Mg	K	Na	Al	Si	NH ₄ -N	NO ₃ -N	PO ₄ -P
Soil (S)	**	**	**	**	*	**	**	**	**	**
pH (P)	**	**	**	**	*	**	**	**	NS	**
Time (T)	**	**	**	**	**	**	**	**	**	NS
SP	**	**	**	**	**	**	**	*	NS	**
ST	**	**	**	**	**	**	**	**	**	**
PT	**	**	**	**	**	**	**	**	*	**
SPT	**	**	**	**	NS	**	**	**	NS	**

Table III The mean extract concentrations averaged over time. Within an element, two means which differ by Tukey's honestly significant difference (hsd) are statistically different.

Soil	Spike		Extract Concentrations (µmoles/l)								
	pH	pH	Ca	Mg	K	Na	Al	Si	NH ₄ -N	NO ₃ -N	PO ₄ -P
Dune Sand	5.6	5.07	0.1	13	17	111	6.1	10	6.0	56	5.1
	4.0	5.06	5	16	14	105	3.9	10	7.2	59	6.5
	2.5	4.77	19	55	15	89	4.2	13	7.0	60	3.0
	1.0	2.52	325	423	51	107	784	210	53	9	41.5
Baywood	5.6	5.43	19	13	52	76	7.6	15	2.0	80	12.8
	4.0	5.39	8	13	54	89	10.5	13	1.7	84	6.1
	2.5	5.15	34	37	65	64	5.0	15	1.2	81	6.3
	1.0	2.76	762	380	201	78	623	228	38	14	13.4
Tangair	5.6	5.27	58	57	76	124	10.0	16	7.1	312	1.8
	4.0	5.33	57	61	81	138	7.3	17	5.9	309	2.3
	2.5	5.13	82	91	99	112	3.1	16	7.3	314	2.1
	1.0	3.71	1793	858	250	130	334	172	94	139	4.2
Santa Lucia	5.6	5.12	82	151	77	550	26	154	15	543	4.3
	4.0	5.07	75	158	69	542	20	135	15	532	2.1
	2.5	4.93	90	182	74	571	19	137	15	550	2.3
	1.0	4.29	1246	2017	293	886	23	205	76	424	1.4
Tukey's hsd (5%)			242	133	71	151	123	29	22	201	6.6

FIGURE LEGENDS

- Figure 1. The total base and carbon content in the surface meter of soil.
- Figure 2. The effect of acid spikes on the soil extract pH.
- Figure 3. The effect of acid spikes on the soil extract Ca.
- Figure 4. The effect of acid spikes on the soil extract K.
- Figure 5. The effect of acid spikes on the soil extract $\text{NO}_3\text{-N}$.
- Figure 6. The effect of acid spikes on the soil extract $\text{PO}_4\text{-P}$.
- Figure 7. The effect of acid spikes on the soil extract Si.
- Figure 8. The effect of acid spikes on the soil extract Al.
- Figure 9. The charge-carrying cations from the extracted soils.
- Figure 10. A comparison of total extracted and exchangeable bases.
- Figure 11. A stability diagram for selected silica, aluminum, and aluminosilicate minerals.
- Figure 12. The relationship between pAl and pH.
- Figure 13. A schematic diagram of the acid neutralization process.
- Figure 14. The depth of soil base depletion as a function of the number of acid additions (183 meq/m^2) (a hypothetical case).

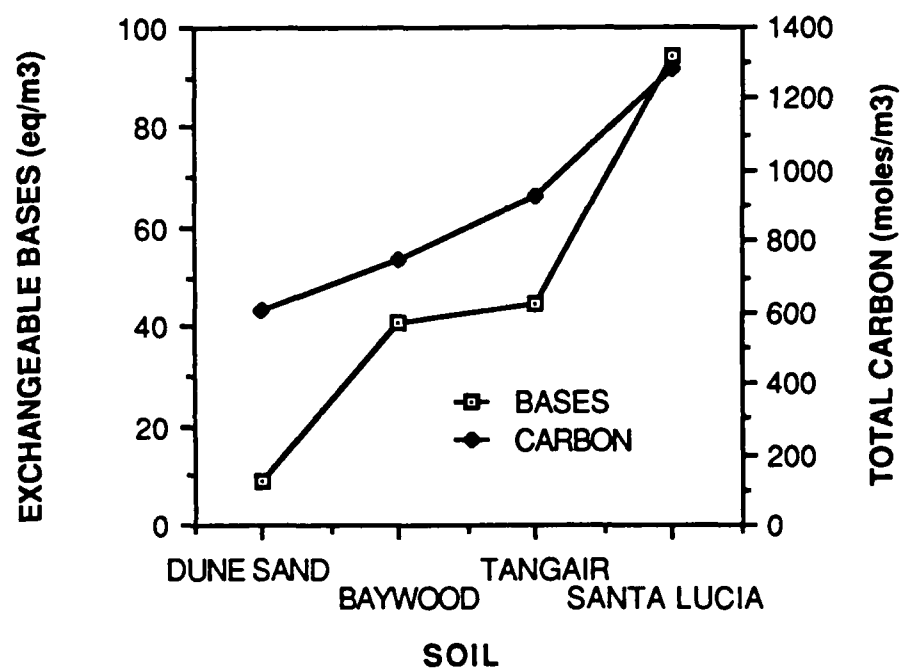
BASES AND CARBON IN SURFACE SOIL METER

Fig. 1

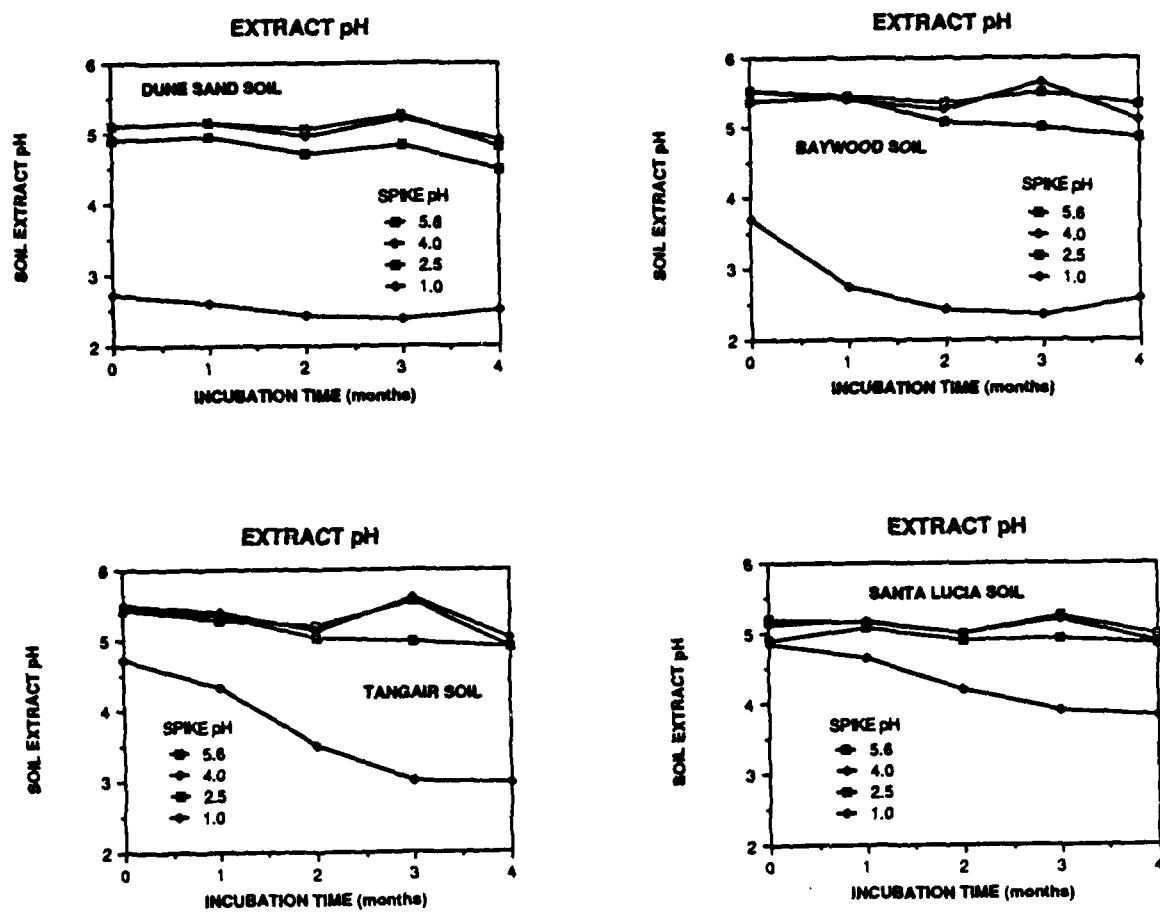


Fig. 2

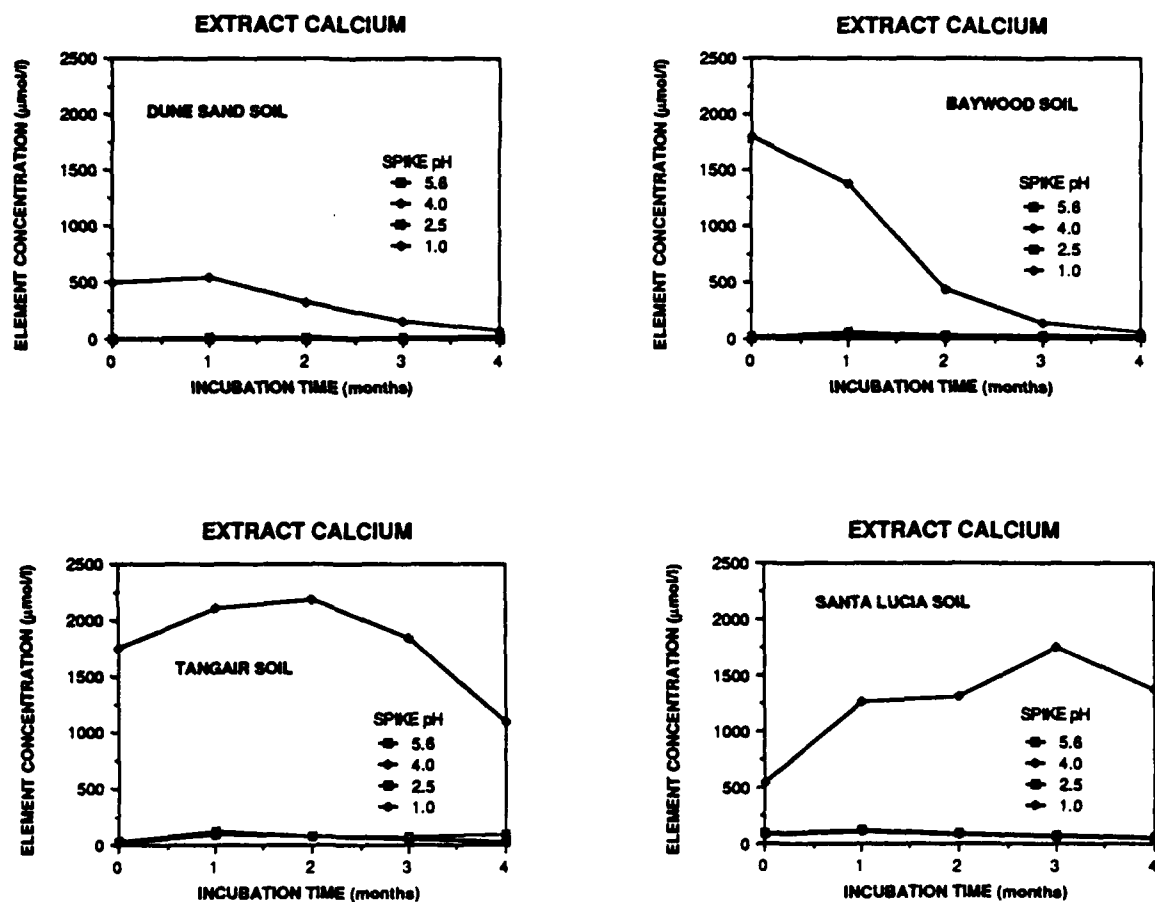


Fig. 3

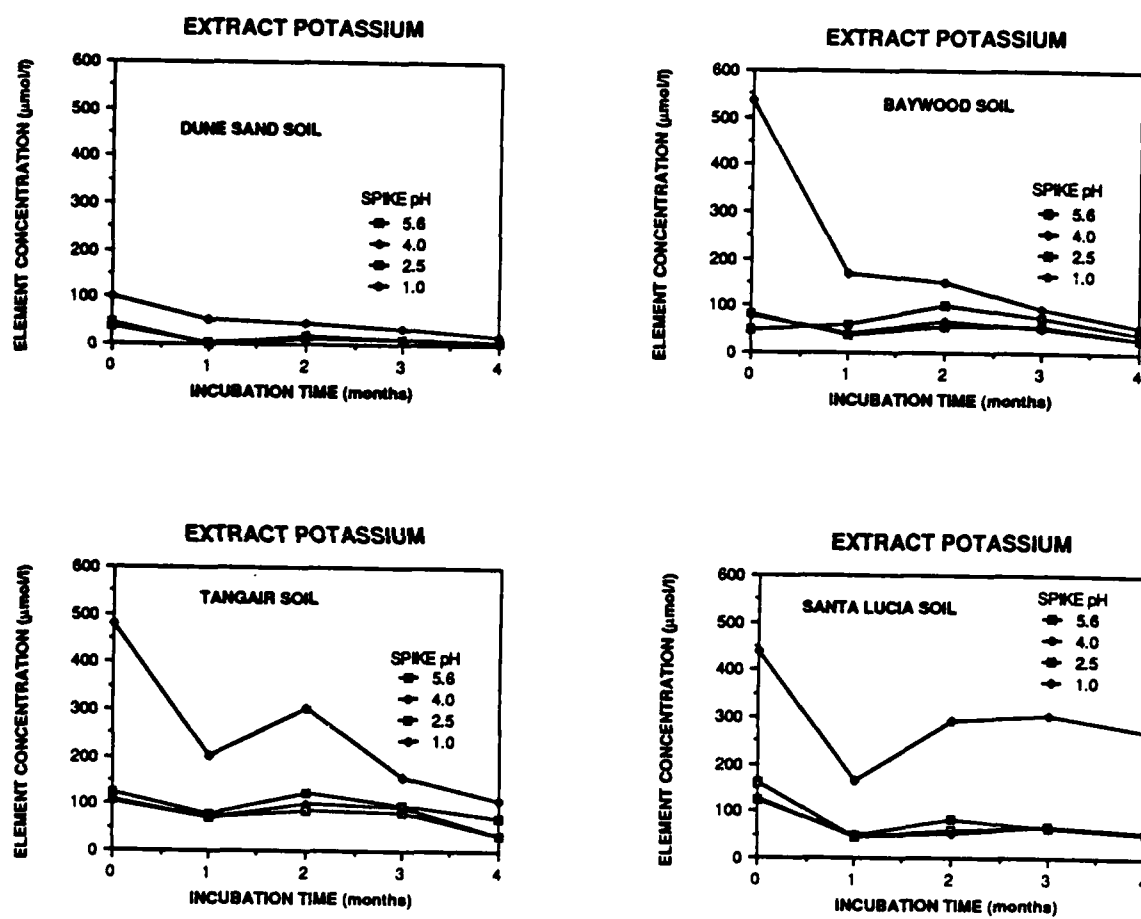


Fig. 4

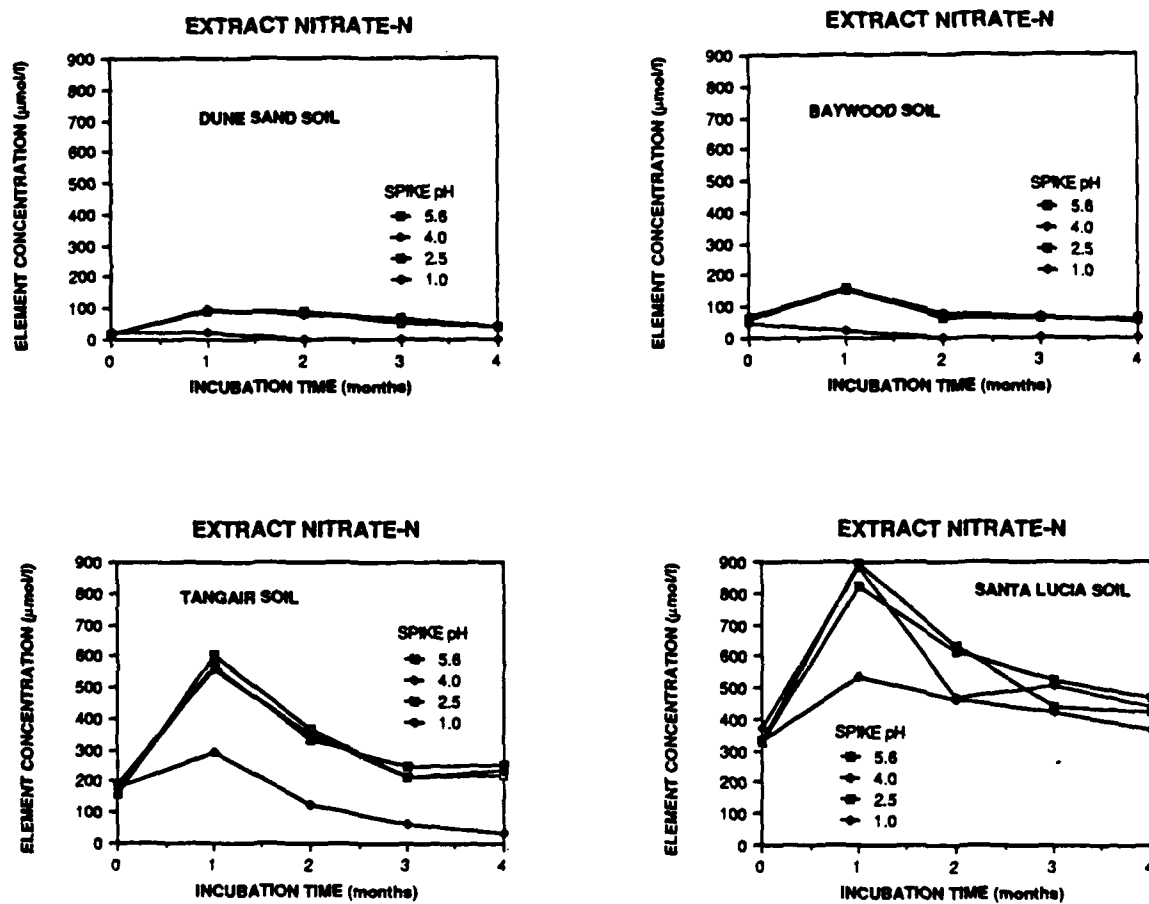


Fig. 5

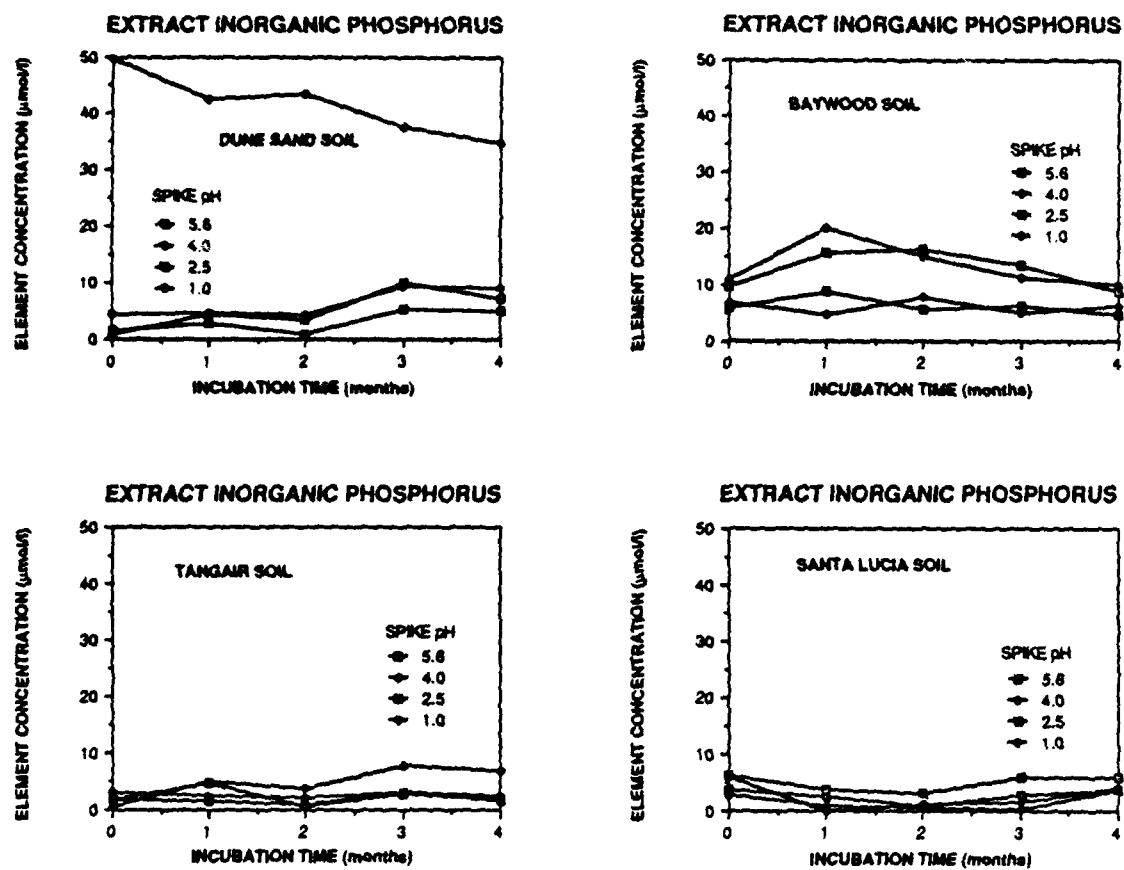


Fig. 6

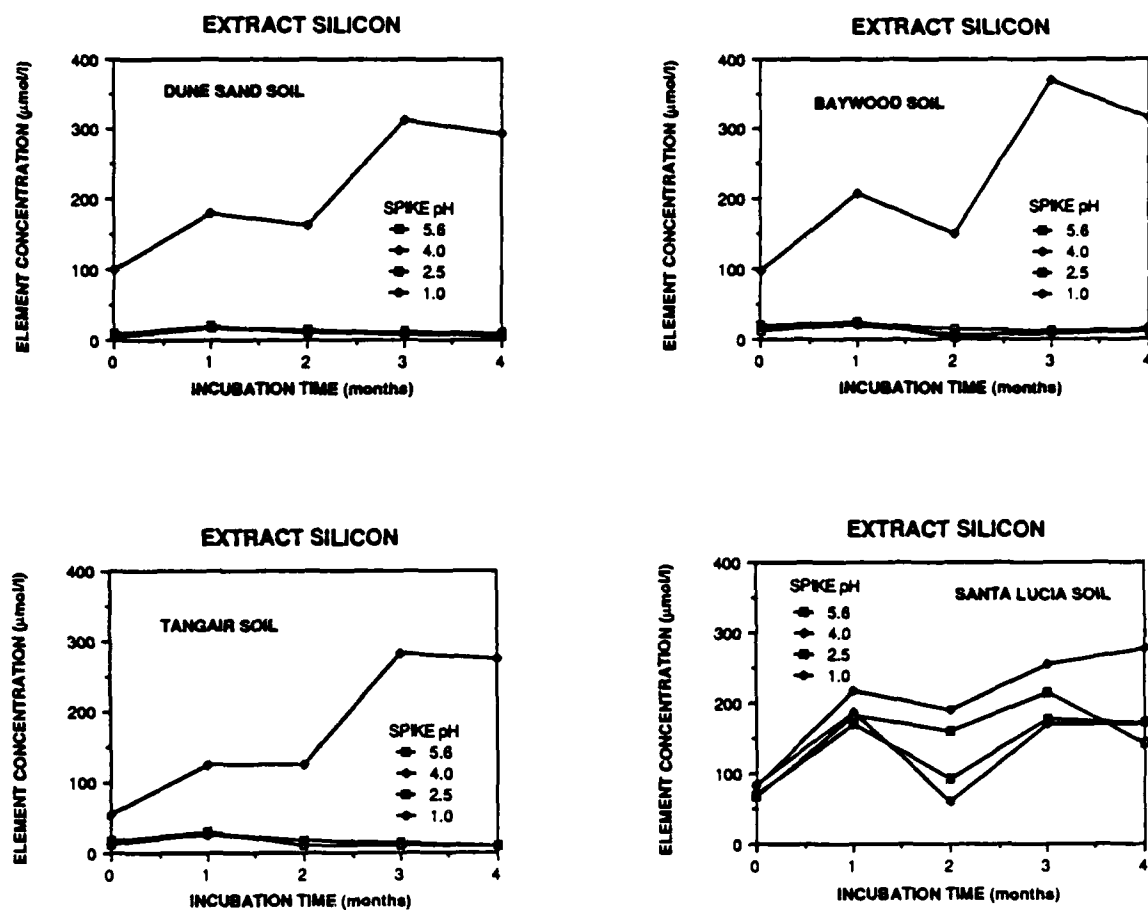


Fig. 7

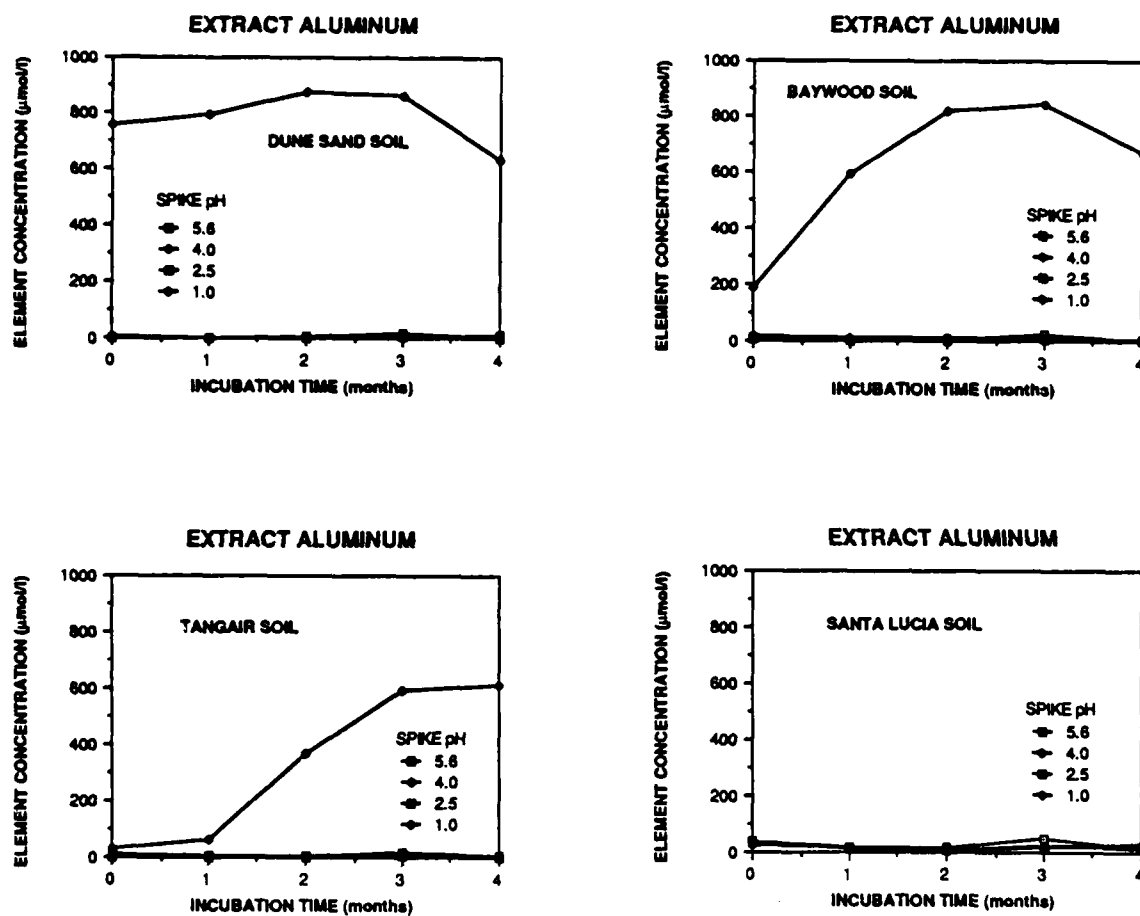


Fig. 8

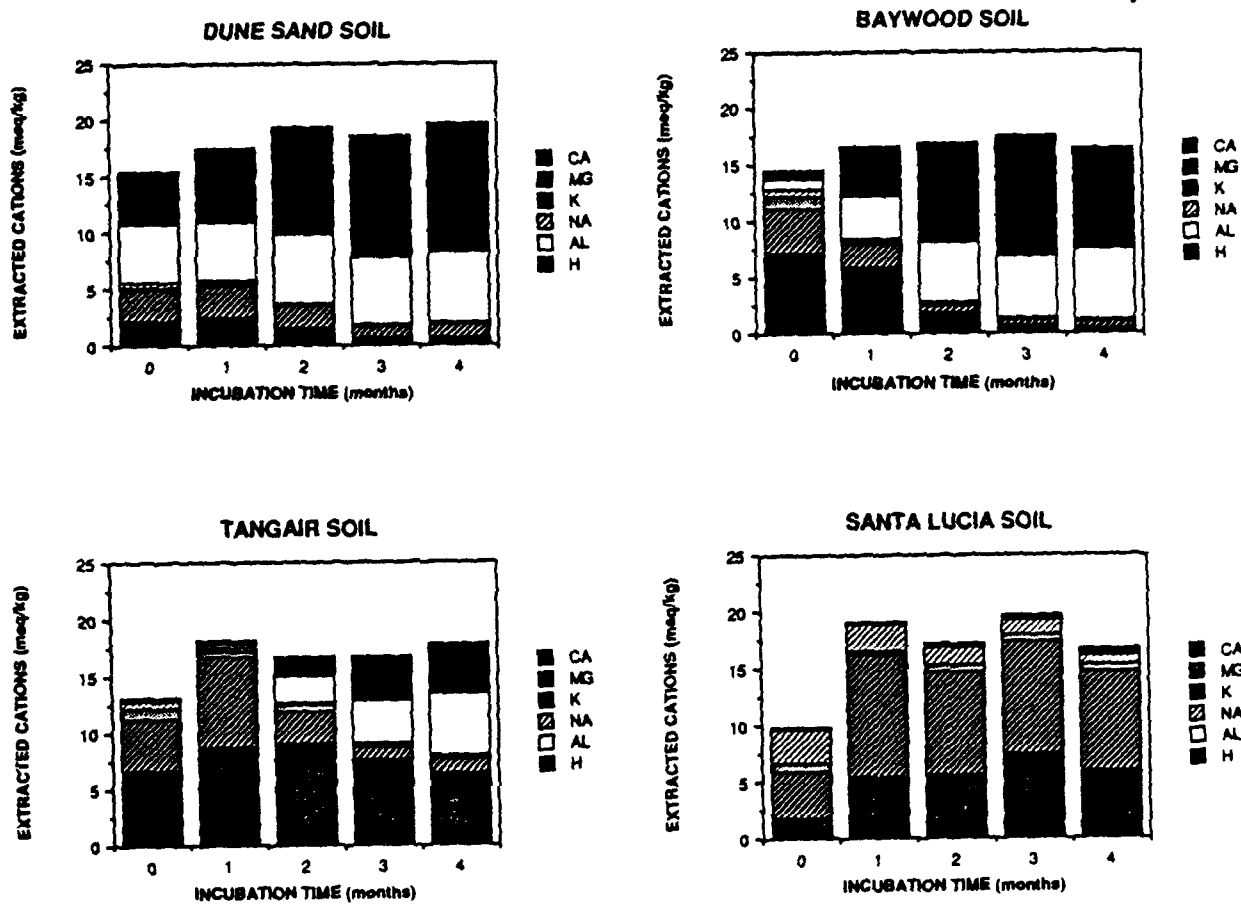


Fig. 9

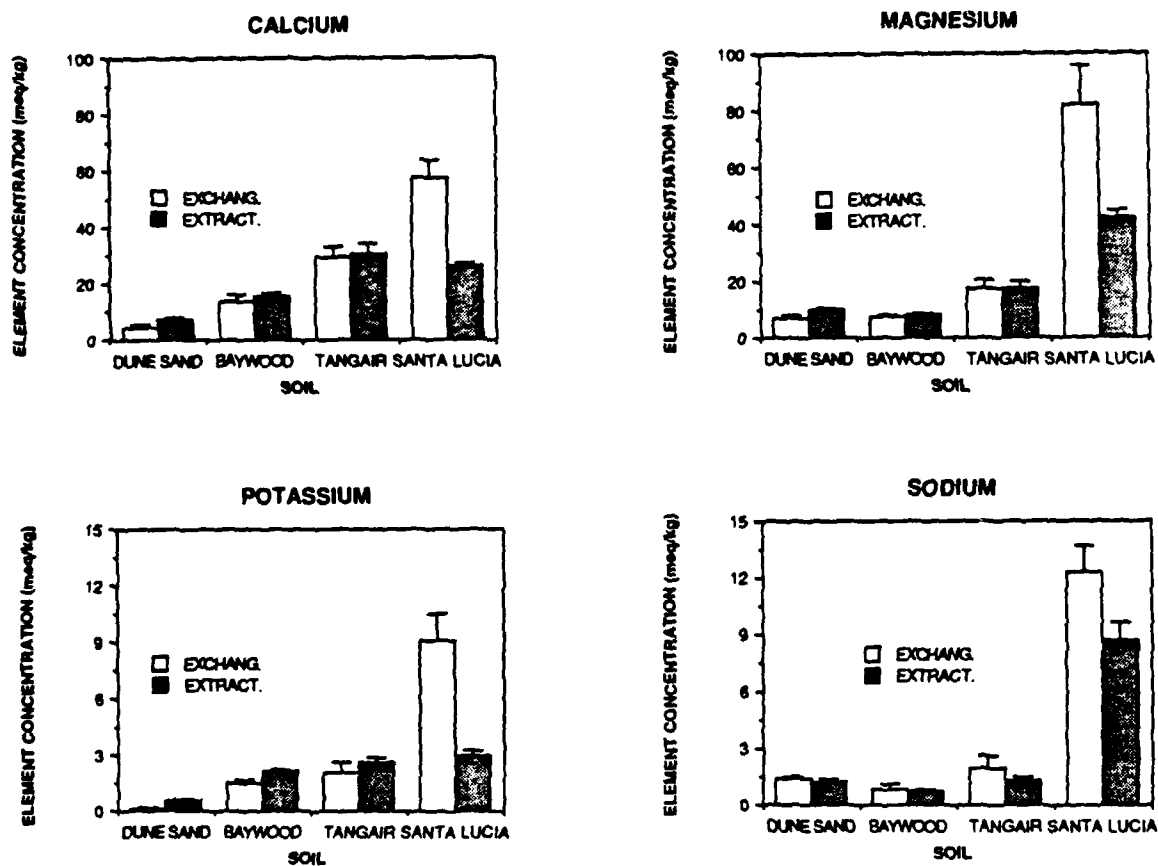


Fig. 10

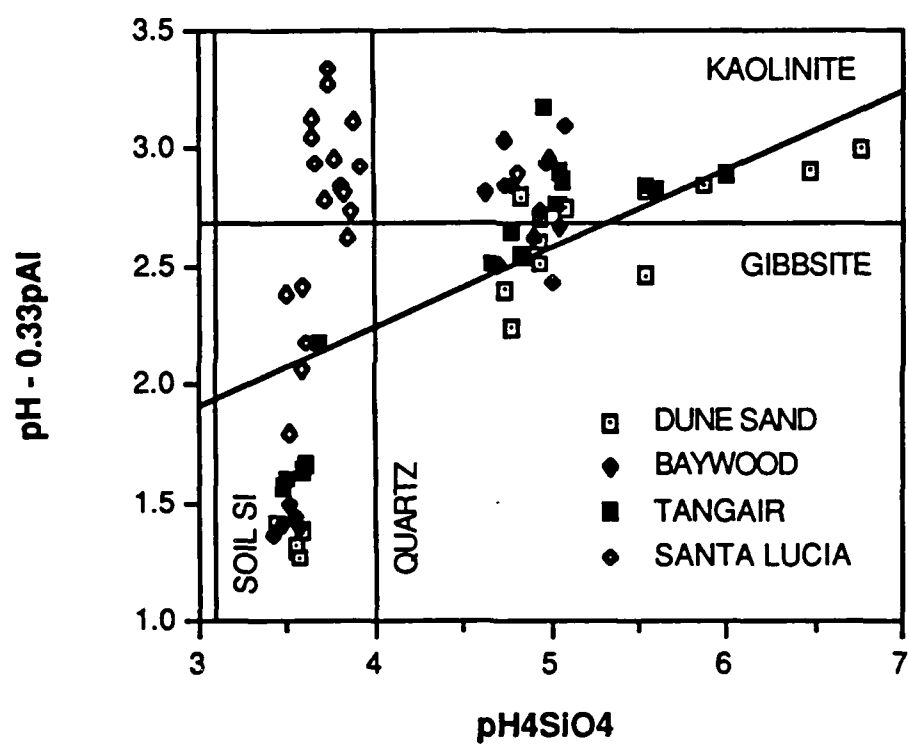


Fig. 11

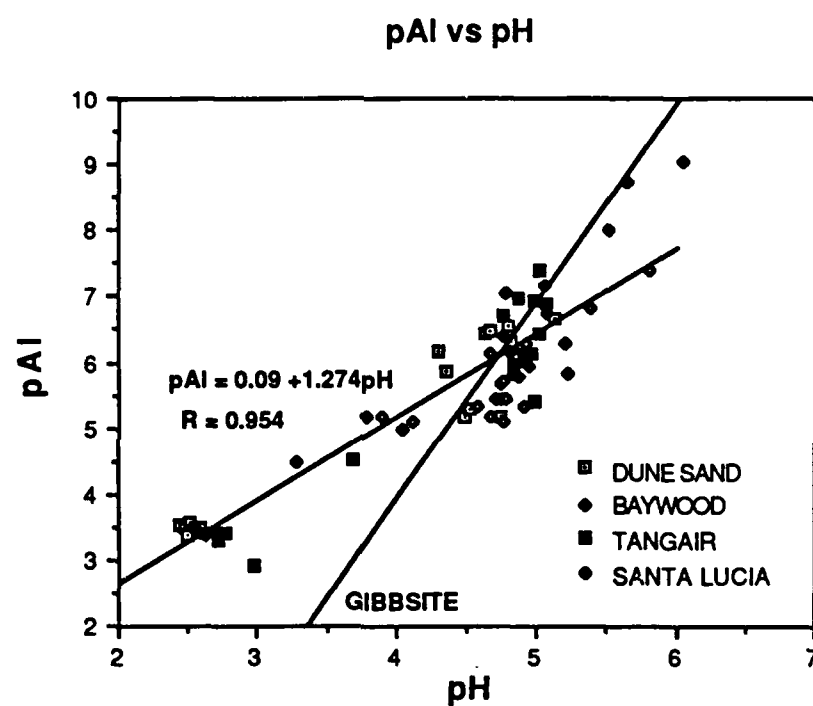
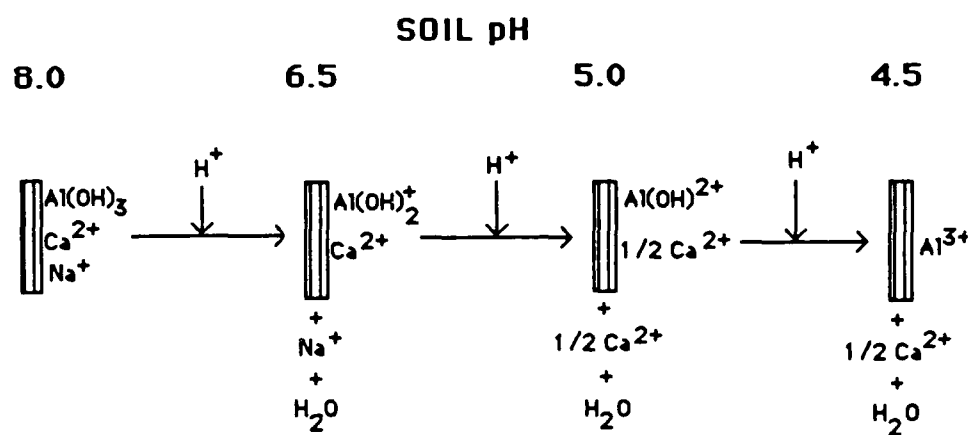


Fig. 12



THE ACID NEUTRALIZATION PROCESS

Fig. 13

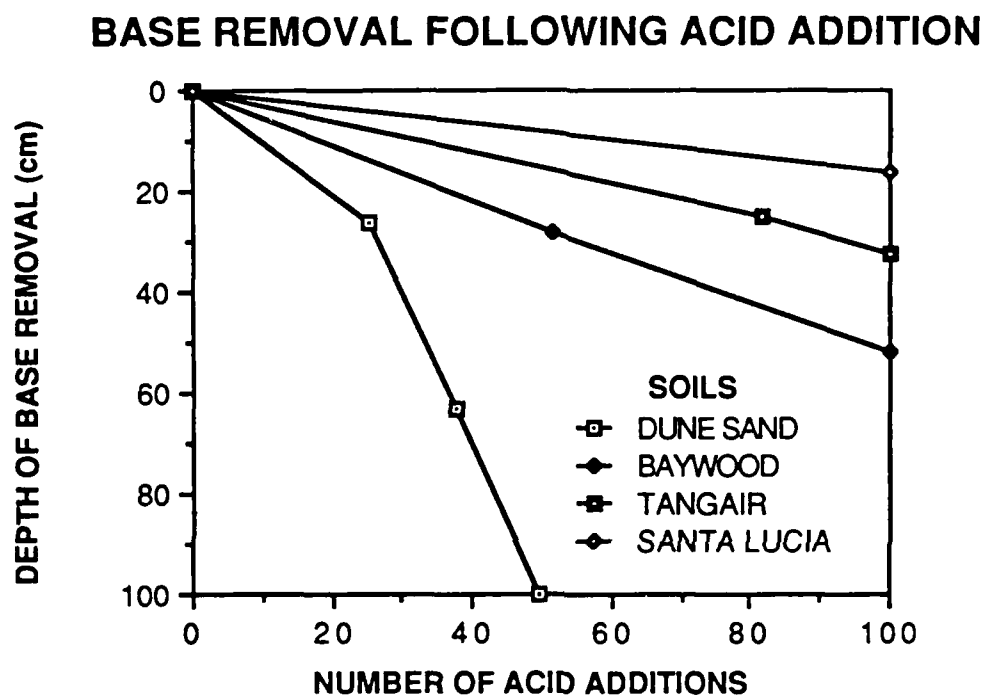


Fig. 14

PART 5

INVASION OF CARPOBROTUS EDULIS AND SALIX LASIOLEPIS AFTER FIRE IN
A COASTAL CHAPARRAL SITE IN SANTA BARBARA COUNTY, CALIFORNIA.

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ABSTRACT

Observations in permanent plots after a 1982 controlled fire in chaparral vegetation in coastal Santa Barbara County, California demonstrate that Carpobrotus edulis, the common introduced ice plant, increased substantially along with other native plants capable of invading disturbed sites such as *Salix lasiolepis*. Although fire is a natural disturbance, it can favor the spread of invasive exotics when a seed source is available. Controlled burning programs must consider the possibility and risks of invasion by exotics.

The importance of human disturbances such as grazing, agriculture, and road construction in promoting the invasion of exotics is well known (Elton 1958). It is less clear if natural disturbance factors such as fire hinder or assist invasion (Johnstone 1986). A well-accepted explanation for weed invasion is that human disturbance creates a new environment in which the native plants are at a disadvantage with respect to invaders. Thus, the argument can be made that fire in a landscape where it has a long history should not give an advantage to exotics. On the contrary, the native plants, which should be fitted to the special local characteristics of the fires, might be favored. This theoretical reasoning is given practical support by burning experiments that have shown a decrease in exotics (e. g., Hillyard 1985). It is the purpose of this paper to demonstrate that burning by no means inevitably favors natives and may, in some instances, promote the spread of exotics.

The exotic studied here, Carpobrotus edulis (L.) Bolus ("ice-plant"), has been widely planted in California and is now viewed as a weed (McClintock 1985) that should be eradicated in sensitive natural habitats (e.g., Libby 1979). It is particularly

aggressive in sandy coastal sites (Griffin 1978), where it can become the dominant plant over large areas. As an exotic and a succulent plant, Carpobrotus edulis populations might be expected to react negatively to burning, and this reaction might offer a means of controlling this species. Our results show that fire may favor its expansion.

STUDY AREA

The study was conducted on Burton Mesa in Santa Barbara County (34° 42' 30" N 120° 43' W) about 2.6 km from the ocean to the west of the railroad tracks near the intersection of 35th street and California boulevard on Vandenberg Air Force Base. The soil type at the site is mapped as Tangair with inclusions of the poorly-drained Narlon series (Shipman 1972). Both soils have coarse sandy loam textures, are derived from marine deposits, and are low in fertility.

The vegetation at the site is a distinctive central-coast phase of chaparral. It is characterized by low, sometimes salt-spray trimmed canopies of evergreen species with an admixture of drought-deciduous coastal sage scrub elements. The site also includes other species of limited or disjunct distribution, such as Arctostaphylos rudis and Eriodictyon capitatum.

METHODS

The data reported here were collected in conjunction with an experimental burn of approximately 40 ha conducted in the summer of 1982 to determine the effect of prescribed fire on E. capitatum (Jacks, Zedler, and Scheidlinger unpub. report.). Before the fire, a sample area of approximately 0.6 ha, delimited by clearing along a paved road, a railroad track, and an old unpaved track, was selected and divided into two plots of about 2500 and 3600 sq. m., the larger of which was left unburned. A 100

meter transect, crossing both the burned and unburned vegetation, was established in June 1982 before the fire and was sampled for crown cover. In addition to marking individual E. capitatum to follow in survivorship studies, we established four 3 x 3 meter plots in the burn area centered on E. capitatum clumps. These plots were therefore not random with respect to E. capitatum but were not selected with reference to C. edulis. The cover of all shrub species within these plots was recorded and the location of all E. capitatum were mapped before the fire. After the fire seedlings and sprouts were mapped.

We estimated seed production of C. edulis in 1985 by counting the number of fruits in 40 regularly spaced meter-square quadrats, collecting 3 fruits from each quadrat in which they were present, and counting the seeds in a randomly selected sub-sample of 12 fruits.

RESULTS

In 1982, before the fire, C. edulis was present along the road and the railway that bordered the site. None was recorded within the experimental area, however, which had a nearly complete cover of living or dead shrub canopies of primarily evergreen species (Table 1). Because of this dense cover, we cannot assert that C. edulis was not present somewhere in the experimental area, but there is no doubt that its total density was negligible. In contrast, in 1985, three years after the fire, the cover of C. edulis was 26%, making it the second-most abundant post-fire perennial plant (Table 1).

Observations in the permanent plots confirm that seedling establishment is responsible for the increase in C. edulis. These plots were resampled in 1983, and the location of C. edulis and shrub seedlings was recorded (Table 2). Seedlings of C. edulis were recorded at an average density of over 7000/ha. A 1985 resample

relocated 70% of these, indicating a high survivorship. Three new plants of C. edulis were found in 1985 that may have been established in the second season of recovery but more probably were missed in the initial survey.

Although C. edulis has been reported to reproduce only vegetatively (McClintock 1985), the observed seedling establishment obviously contradicts this. We collected fruits and found an average of 5.3 (SD 12.1, N=40) fruits/m² and an average of 1004 seeds/fruit (SD 431, N=12). This indicates a 1985 seed production of over 5.3 million seeds/ha. Obviously this figure will vary from year to year and place to place, but the numbers serve to show that C. edulis can have prodigious seed production.

The establishment of several other species is also indicative of the susceptibility of burned chaparral to invasion. The presence of seedlings of Salix lasiolepis in the burned area was very unexpected (Table 2). No mature individuals of this species were observed anywhere within a kilometer of the site before or after the fire. The identity of the species was confirmed, however, by comparison with seedlings found along the Santa Ynez River, where the species is very abundant. We assume that the seeds were blown onto the site from these large stands along the Santa Ynez River which lies about 2 km to the south.

It is not surprising that willow seeds dispersed to the site and germinated there. What is more remarkable is that they established and survived to early July 1983, and that a few were still present and alive in the area the following summer. The mortality in the permanent plots was, however, complete by the second summer. The initial survival of the willows probably was aided by the fact that the 1982-83 hydrologic year for the area was one of above normal precipitation (81.9 cm; mean rainfall is 35.2 cm), and it may have been enhanced by the presence of a heavy clay layer overlying shale bedrock that underlies the sandy surface soil at a depth of a

meter or more. This may have allowed high moisture conditions to persist over the first summer. This wet year was followed by two years of below average precipitation (1983-84, 21.6 cm; 1984-85, 26.5 cm) which, in part, may explain the lack of willow establishment.

Other exotic species besides C. edulis were observed in the post-burn area. A number of Eucalyptus sp. seedlings, whose seeds evidently dispersed from a nearby windbreak, were present as were clumps of Cortaderia sp. and Herrea elongata, an exotic succulent introduced from South Africa.

Two easily dispersed native species, Baccharis pilularis (wind) and Solanum xantii (animal) were common as seedlings in the post-fire vegetation (Table 2) even though they were minor elements as mature shrubs before the fire. These species are frequent in chaparral and coastal sage scrub, and it is questionable whether their presence constitutes "invasion".

DISCUSSION

The substantial cover of C. edulis after the 1982 fire is evidence that the invasion of exotic species into native vegetation can be advanced, rather than retarded by burning. This is all the more remarkable because as a succulent and as a coastal plant C. edulis did not seem to us to be a species that would benefit from burning. The plants of this genus appear to be able to do this not only in California, but also in its native habitats in South Africa and Australia. Eugene Moll (pers. comm. 1985) of the University of Cape Town has noted seedling establishment of C. dinidiata after fire in the sand plain and mesic mountain fynbos communities in South Africa, although he notes that the species is most abundant in communities that are seldom burned. Judith Brown of the Western Australian Wildlife Research Centre (pers. comm. 1985) reports that C. edulis, also introduced into W. Australia,

establishes by seed after hot fires in coastal locations near Perth, although in her opinion it is "not an aggressive colonizer". She notes, however, that native species of Carpobrotus can invade woodlands after fire. In one case on Middle Island off the coast of W. Australia a thick carpet of Carpobrotus developed from seedlings after fire in a Eucalyptus angulosa-E. platypus forest unburned for 170 years. This evidence suggests that invasion of C. edulis into burned chaparral at Vandenberg AFB may not be as anomalous as it appears.

Although fire provided the "temporary invasion window" (Johnstone 1986) there must also be propagules to exploit it. We do not know how and when the seeds of C. edulis dispersed to the site. Fruits of C. edulis are eaten by small mammals (W. Ferren, pers. comm.) and the seeds are small and hard-coated. We suspect that most of the seeds were deposited at the site in small mammal feces. Therefore, the majority of the seeds probably were in the soil for some time before the fire.

It is known that fire can be used to decrease exotics in coastal settings. W. James Berry of the State Department of Parks and Recreation (pers. comm. 1985) reports several successes in controlling introduced species--Avena at Pt. Mugu and Malibu, Bromus diandrus at Montana de Oro, and Brassica at Pt. Lobos. Timing was a key element in these efforts. The burns were conducted when they would kill most of the seed crop of the exotics without seriously harming the desirable species, mostly perennial natives.

Our observations make it clear that these successes must not be taken as an indication that fire will inevitably act to the favor of natives over exotics. A case in point comes from South Africa where the native vegetation is well adapted to survive fire, but invasion of exotics, including pines from the Northern Hemisphere and Hakea from Australia, has become a serious problem. Fire can be

used to reduce the abundance of some of these the invaders, but others (e.g., Acacia) cannot be eliminated with burning (Kruger and Bigalke 1984).

It is also apparent that edge effects were important in the situation we describe. Human disturbance along the margins of the experimental plot allowed the populations of C. edulis to establish and maintain themselves. Fire provided the opportunity for the seedlings to establish. These results underline the importance of minimizing edge to area ratios in retarding the expansion of exotics. They also suggest that longer fire rotations should be favored over shorter rotations in situations where exotics that can exploit open conditions are already part of the system. Coastal sage scrub communities are particularly vulnerable to changes in species composition (i.e. invasion) when, as in this case, the vegetation is composed mainly of species with no ability (e.g. *Ceanothus* spp., *Arctostaphylos* spp.) or only a weak ability (e.g. *Salvia mellifera*, *Eriodictyon capitatum*) to resprout after fire (Westman and O'Leary 1986).

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LITERATURE CITED

- Elton, C.S. 1958. The Ecology of Invasions by Animals and Plants. Chapman and Hall, London.
- Griffin, J.R. 1978. Maritime chaparral and endemic shrubs of the Monterey Bay region, California. *Madrono* 25:65-112.
- Hillyard, D.S. 1985. Weed management in California's State Park System. *Fremontia* 13:18-19.
- Johnstone, I.M. 1986. Plant Invasion Windows: A time-based classification of invasion potential. *Biol. Rev.* 61:369-394.
- Kruger, F.J. and R.C. Bigalke 1984. Fire in fynbos. In P. de V. Booysen and N. M. Tainton (eds.), *Ecological Effects of Fire in Southern Africa Ecosystems*, Chapter 5. pp. 67-114. Springer-Verlag, Berlin.
- Libby, J. 1979. Chapter Weed Reports: Acacia and Pampas grass in Santa Cruz. *Fremontia* 6:19-20.
- McClintock, E. 1985. Escaped exotic weeds in California. *Fremontia* 12:3-6.
- Shipman, G.E. 1972. Soil survey of the northern Santa Barbara area. U.S.D.A. Soil Conservation Service, Washington, D.C.

Smith, C.F. 1976. A Flora of the Santa Barbara Region, California. Santa Barbara Museum of Natural History, Santa Barbara, California.

Westman, W.E. and J.F. O'leary 1986. Measures of resilience: The response of coastal sage scrub to fire. *Vegetatio* 65:179-189.

Table 1. Pre- and post burn cover of shrubs, sub-shrubs, and Carpobrotus edulis on a chaparral site on Vandenberg Air Force Base, Santa Barbara County, California. Transect lengths were 60 meters for 1982 and 100 meters for 1985. Live cover values include overlap. Bare ground is area not covered by live or dead plant canopies. Nomenclature after Smith (1976).

Species	Pre-Burn 1982 Cover (%)		Post-Burn 1985 Cover (%)	
	Live	Dead	Live	Dead
<u>Adenostoma fasciculatum</u>	45.3	1.2	4.3	0.0
<u>Arctostaphylos purissima</u>	39.3	0.3	1.1	0.0
<u>Arctostaphylos rudis</u>	15.9	1.7	1.0	0.0
<u>Carex sp.</u>	0.0	0.0	0.3	0.0
<u>Carpobrotus edulis</u>	0.0	0.0	26.2	0.3
<u>Ceanothus impressus</u>	0.0	0.0	0.1	0.0
<u>Ceanothus ramulosus</u>	1.2	2.6	0.5	0.0
<u>Eriodictyon capitatum</u>	3.2	1.2	1.7	0.0
<u>Haplopappus ericoides</u>	1.0	0.1	0.0	0.0
<u>Helianthemum scoparium</u>	0.0	0.0	30.4	1.9
<u>Lotus scoparius</u>	0.0	0.0	3.0	0.9
<u>Salvia mellifera</u>	3.9	0.4	3.6	0.0
Bare ground	1.8	—	33.1	---

Table 2. Abundance of seedlings in permanent quadrats noted in July 1983 after the summer 1982 prescribed burn. Values are based on averages of four 3 x 3 m plots. S.E. represents the standard deviation of the mean for the sample of four plots.

Species	number/ha	S.E.
Arctostaphylos rudis	2230	4450
A. purissima	41075	18000
Adenostoma fasciculatum	1650	1650
Salvia mellifera	6930	2700
Ceanothus ramulosus	825	830
C. impressus	1375	1380
Salix lasiolepis	6400	715
Baccharis pilularis	4425	1211
Lotus scoparius	3600	1895
Carpobrotus edulis	7780	2100
Solanum xantii	4700	1470

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